0, 11, US8
no 3292

LIBRARY
FISH & WILDLIFE SERVICE
PACIFIC OCEANIC FISHERY
INVESTIGATIONS
APR 1 1952

# A STUDY OF AN INTERMEDIATE SNAIL HOST (THIARA GRANIFERA) OF THE ORIENTAL LUNG FLUKE (PARAGONIMUS)

BY

R. TUCKER ABBOTT

No. 3292.—From the Proceedings of the United States National Museum
Vol. 102, pp. 71–116, pls. 8, 9, figs. 32–45

SMITHSONIAN INSTITUTION
UNITED STATES NATIONAL MUSEUM
WASHINGTON, D. C.
1952

PROCEEDINGS OF THE UNITED STATES NATIONAL MUSEUM

issued by the

SMITHSONIAN INSTITUTION
U. S. NATIONAL MUSEUM

Vol. 102 Washington: 1952 No. 3292

# A STUDY OF AN INTERMEDIATE SNAIL HOST (THIARA GRANIFERA) OF THE ORIENTAL LUNG FLUKE (PARAGONIMUS)

By R. Tucker Abbott

In recent years there has been increasing interest in the Thiaridae, or "melaniid" snails, not only among students of mollusks but also among parasitologists, for numerous species in this family serve as the intermediate hosts of human trematode diseases. A few years ago *Thiara granifera* (Lamarck), an important intermediate snail host of the Oriental lung fluke (*Paragonimus westermani* Kerbert), was accidentally introduced and has established itself in Lithia Spring, Fla. As an aid to public-health workers and parasitologists, the anatomy, the bionomics, the manner of introduction, and the details of identifying characters of this species are given in this paper. There was also a need for a study of the gross morphological features of and ecological variations in *Thiara*, before an attempt could be made to solve the problems of speciation and systematic relationships of the genus.

This study was begun on Guam Island, the Marianas, and the Philippine Islands, where field observations and collecting were carried on from May 1945 to January 1946. Further field study was undertaken under the auspices of the Smithsonian Institution in January and February of 1948 at Lithia Spring, Hillsborough County, Fla., where bionomic studies were made on several introduced colonies of this species. Most of the anatomical work was done in the division of mollusks, United States National Museum, where these collections are now housed. Paraffin embedding and sectioning of animals was done in the Department of Zoology at George Washington University.

I wish to thank Albert Greenberg, of the Everglades Aquatic Nurseries in Tampa, for his many kindnesses in connection with the field work.

## SYSTEMATIC POSITION

This paper is primarily a study of the anatomy and the life history of the fresh-water snail *Thiara granifera.* Although much material from all parts of the Pacific region has been critically examined, it is felt that a detailed analysis and presentation of the various subspecies and related species is a task at present beyond the scope of this study. However, a brief systematic orientation is included here for those wishing to use this anatomical study for comparative work:

| | |
|---|---|
| Phylum: | MOLLUSCA |
| Class: | GASTROPODA |
| Order: | PROSOBRANCHIATA, Suborder TAENIOGLOSSA |
| Family: | THIARIDAE (=MELANIIDAE) |
| Subfamily: | THIARINAE |
| Genus: | *Thiara* Röding, 1798 |
| Subgenus: | *Tarebia* H. and A. Adams, 1854 |
| Species: | *granifera* Lamarck, 1816 |

The genus *Thiara* Röding, 1798, more familiarly known in older literature as *Melania* Lamarck, 1816, is represented by some fewer than 100 named species and forms, all of which are from the warmer regions of southern Asia, the East Indies, and the larger Pacific islands. As more and more species were described subgeneric names were proposed, such as *Plotiopsis*, *Tarebia*, *Melanoides*, and *Tiaropsis*, and these were later raised to generic standing. Recently there has been a tendency in the opposite direction, to recognize fewer species and to include these subgenera under the single genus *Thiara* (Abbott, 1948). The subgenus *Tarebia* H. and A. Adams, 1854, contains such species as *granifera* Lamarck, *rudis* Lea, and over two dozen names of subspecific or doubtful varietal rank. The specimens that have been used in this anatomical study came from Guam Island, in the Marianas, and are most likely members of a widespread race of *Thiara granifera*, which was given the name of *mauiensis* by Lea in 1856.

## GENERAL DESCRIPTION

*Thiara granifera* is a relatively small gastropod, in which adults may vary in shell length from 6.0 to 40.0 mm., although the commonest size is approximately 25.0 mm. (one inch). The shell is rather elongate with a straight-sided, pointed spire and is sculptured with several spiral rows of beads or blunt tubercles. The aperture of the shell is obliquely ovate, and the apertural lip is sharp. The color of the shell and its thin periostracal covering is generally a light brown to yellowish brown, which sometimes is flecked with small, dark, red-

brown color spots. The operculum is about two-thirds the size of the aperture, opaque, and colored a dark blackish brown. The animal and operculum may be withdrawn into the shell completely from view. When fully extended the head and foot are, together, about one-fourth the length of the shell. The foot is relatively small and square to oblong. The proboscis is rather large and flattened. The two tentacles are round and slender and extend slightly beyond the anterior limits of the proboscis. The mantle, which lines the interior of the last shell whorl, is bordered by several prominent, fleshy papillae, which may be seen projecting beyond the shell lip on the left (or outer lip) side. In mature and gravid specimens a brood pouch is present on the back of the animal just behind the head. In some individuals the shells of the small, living young may be seen through the thin dorsal wall of the pouch.

## EXTERNAL ANATOMY

Shell (pl. 8, figs. 1, 2): Many minor geographical variations occur in the shell characters of this species, and since some confusion is apt to result if a composite description of the various races is presented, I have limited my remarks to a single colony, which was collected on October 8, 1945, near the reservoir dam, Geus River, Guam Island, Marianas (U.S.N.M. No. 590182). Supplementary remarks are appended concerning the shell differences between the Guam colonies and the population samples from Lithia Spring, Fla.

Shell elongate-turrite, from 15.0 to 25.0 mm. in length, relatively thin but strong. Color yellowish brown. From 7 to 11 whorls. First 3 or 4 whorls reddish brown with microscopic raised spiral threads and rather stronger, retractively slanting, axial riblets, which increase in strength on the succeeding whorls. Periphery of whorls nearly flat, but becoming slightly more rounded in last whorls of specimens over 20.0 mm. in length. Spire pointed and cast at an angle of from 31° to 35°. Suture well impressed, slightly irregular. Base of body whorl very slightly rounded and cast approximately 35° from the axis of the shell. Spiral sculpturing consists of 4 to 6, though most commonly 5, rows of round to squarish, small beads. In later whorls the lower 3 or 4 rows of beads become flattened and often fuse to form a single raised, smooth spiral band. Beads of top row have a tendency to become more pointed and tuberculate. Last whorl, including base of shell, bears 12 to 14 spiral rows, although the lower 10 are nearly always simple, raised bands without beads. Sharply incised, fine, spiral lines may be developed on any of the whorls and, when occurring on the tops of the beads, may in the following whorls become deeper and wider, and finally spread apart what was originally one row of beads into 2, 3, or rarely 4 rows. These incised lines occasion-

ally disappear, allowing split beads to re-fuse into a single row. Many exceedingly fine, incised lines rarely may be present between the rows of beads. Axial sculpture consists of fine, irregular lines of growth which may be prominent, especially in last whorl, at various distances behind lip. Some specimens show a few rather regular, but very small pimplings. In general, the variations mentioned above may appear or disappear at random throughout ontogenetic development. Aperture oblique, moderately ovate to elongate, with a length about one-third that of entire shell. Parietal wall glazed with a transparent, thin covering of shell matter. Columella short, slightly arched, rounded within aperture but sharp on its outer and lower edge. Umbilicus absent. Outer lip thin, sharp, and projecting forward at its center portion. Interior of aperture glossy, chalky white. Periostracum covering entire outer shell (except for parietal wall and columella) thin, closely cemented to shell, yellowish brown. It is most frequently worn away at spire and regions overlying the more prominent beads. Inlaid in the shell itself there are a few small, squarish color-blotches of red-brown, which are usually more easily seen in younger specimens than in adults.

Description of a newly born specimen (pl. 9): Length 2.0 mm., width 1.0 mm. Nuclear whorls rosy pink, finely granulated. Total number of whorls 4.5. Spiral sculpturing in postnuclear whorls con-

TABLE 1.—*Measurements of shells from Geus River, Guam Island*

| Entire shell | | Aperture | | Angle of spire |
|---|---|---|---|---|
| Length | Width | Length | Width | |
| *Mm.* | *Mm.* | *Mm.* | *Mm.* | ° |
| 25. 5 | 10. 8 | 11. 4 | 7. 3 | 30. 5 |
| 25. 2 | 10. 6 | 11. 0 | 7. 5 | 33. 0 |
| 24. 9 | 10. 6 | 10. 5 | 7. 5 | 30. 5 |
| 23. 7 | 10. 0 | 10. 4 | 7. 1 | 32. 0 |
| 24. 1 | 10. 4 | 10. 7 | 7. 0 | 35. 0 |
| 23. 6 | 9. 9 | 10. 6 | 7. 0 | 29. 5 |
| 21. 8 | 9. 1 | 9. 5 | 6. 0 | 29. 5 |
| 19. 3 | 8. 4 | 8. 8 | 5. 3 | 35. 0 |
| 19. 2 | 8. 4 | 8. 3 | 5. 9 | 29. 5 |
| 18. 0 | 8. 0 | 8. 0 | 5. 4 | 29. 0 |
| 16. 3 | 6. 8 | 6. 8 | 4. 9 | 28. 0 |
| 15. 8 | 6. 5 | 6. 8 | 4. 5 | 32. 5 |
| 15. 6 | 6. 4 | 7. 0 | 4. 7 | 30. 0 |
| 13. 5 | 5. 4 | 5. 5 | 4. 2 | 32. 0 |
| 12. 2 | 5. 0 | 5. 1 | 3. 5 | 33. 0 |
| 11. 6 | 4. 8 | 4. 9 | 3. 4 | 36. 5 |
| 10. 6 | 4. 5 | 4. 8 | 3. 2 | 34. 0 |
| 9. 5 | 4. 0 | 3. 9 | 2. 8 | 37. 0 |
| 8. 4 | 3. 5 | 3. 6 | 2. 4 | 33. 0 |
| 14. 8 | 6. 0 | 6. 4 | 4. 3 | 33. 0 |
| 24. 5 | 9. 7 | 9. 7 | 6. 3 | 29. 0 |
| 20. 6 | 8. 3 | 8. 8 | 5. 7 | 30. 0 |

sists at first of two minute, rough threads, increasing to 9 threads in fourth whorl. Axial sculpture on each whorl consists of 11 evenly spaced, raised ribs, which are slightly protractively slanting and are crossed by the spiral threads to form 5 rows of tiny beads on each rib. Ribs absent on lower half of whorl. Suture well indented. Whorls moderately rounded. Umbilicus absent. Columella slightly curved and thin. Outer lip thin and with a sharp, delicate edge. The spire is cast at an angle of 30°.

Measurements of a sample population from Geus River, Guam Island (U.S.N.M. 590182) are given in table 1.

A more detailed biometric treatment is presented in the section dealing with bionomics (p. 99), and figure 32 is a graphic representation. Total shell length has been arithmetically plotted against the

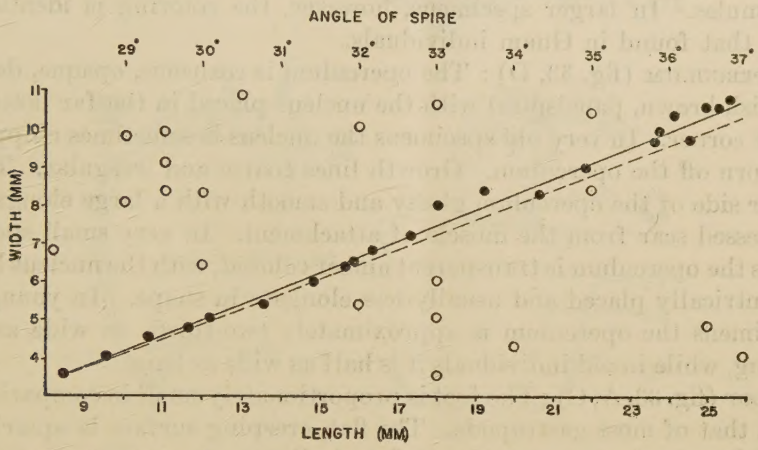


Figure 32.—Correlation between length and width of shell and between angle of spire and width.

width of the shell (solid circles). It will be seen from this graph that the proportion of shell length to width, or the obesity, remains essentially the same throughout life. The slightly more scattered results in larger specimens are probably accounted for by the fact that stream erosion has worn down the first one or two whorls. The unbroken line has been run through the mode of all the correlations. The course of the dotted line has been run through only the six youngest specimens, which showed little or no erosion, and has been protracted farther on to what should be the proper and theoretical ratio for older specimens. It will be noted that the majority of larger specimens are above this dotted line, a phenomenon that has resulted from the reduction of the total length of the older specimens by erosion. The two circles that rest on the dotted line in the larger brackets were not significantly eroded. A more detailed analysis of erosion and methods for its correction have been presented in the section on bionomics (p. 105).

As is shown on the graph by the open circles, which are plots of shell width against angle of spire, there is no correlation between the size, hence age, of individuals and the angle of the spire. Not only is there a marked variation in spire angles but there appears to be a minor, random fluctuation of this angle in the same individual during its life. When this occurs, the sides of the spire are not flat but are either slightly convex or concave. The mean angle of spire for 23 specimens was 31.93°. However, measurements of spire angles are difficult to make, and on the whole are not altogether reliable.

The shells of the Lithia Spring populations closely resemble those of Guam Island, except in being considerably smaller (see under bionomics, p. 104). The red spottings of the Lithia Spring populations are more pronounced and tend to amalgamate axially into small flammules. In larger specimens, however, the coloring is identical with that found in Guam individuals.

Operculum (fig. 33, D) : The operculum is corneous, opaque, dark reddish brown, paucispiral with the nucleus placed in the far bottom right corner. In very old specimens the nucleus is sometimes chipped or worn off the operculum. Growth lines coarse and irregular. The inner side of the operculum glossy and smooth with a large elongate, depressed scar from the muscle of attachment. In very small specimens the operculum is transparent amber colored, with the nucleus less excentrically placed and usually less elongate in shape. In younger specimens the operculum is approximately two-thirds as wide as it is long, while in old individuals it is half as wide as long.

Foot (fig. 33, A, C) : The foot is proportionately small in comparison with that of most gastropods. The flat, creeping surface is squarish, straight edged at its anterior end and slightly truncate posteriorly. The operculum is attached to the dorsal surface at the posterior end. Above this, and continuous with the general musculature of the foot, is the heavy, curved columellar muscle, which is attached to the inner columella of the shell. The anterior, leading edge of the foot bears across its entire width a narrow mucus slit. From this exudes a mucus, which aids the foot in sliding over sand or mud. Immediately above and continuous with the thick foot are the head and proboscis.

Head (fig. 33, A) : The head is ill defined but may be said to include that region posterior to the proboscis that bears the two tentacles, and it contains the brain or central ganglia. Immediately posterior to it, in mature and gravid individuals, lies the brood pouch for the ovoviviparous young. The tentacles are a little longer than the proboscis, round, filiform, and very slightly swollen at the base, where the small black eye is located. The tentacles are capable of being swung in an arc of about 45° in any direction but are rarely bent, curved, or coiled to any great degree. Upon stimulation they may be shrunk to half

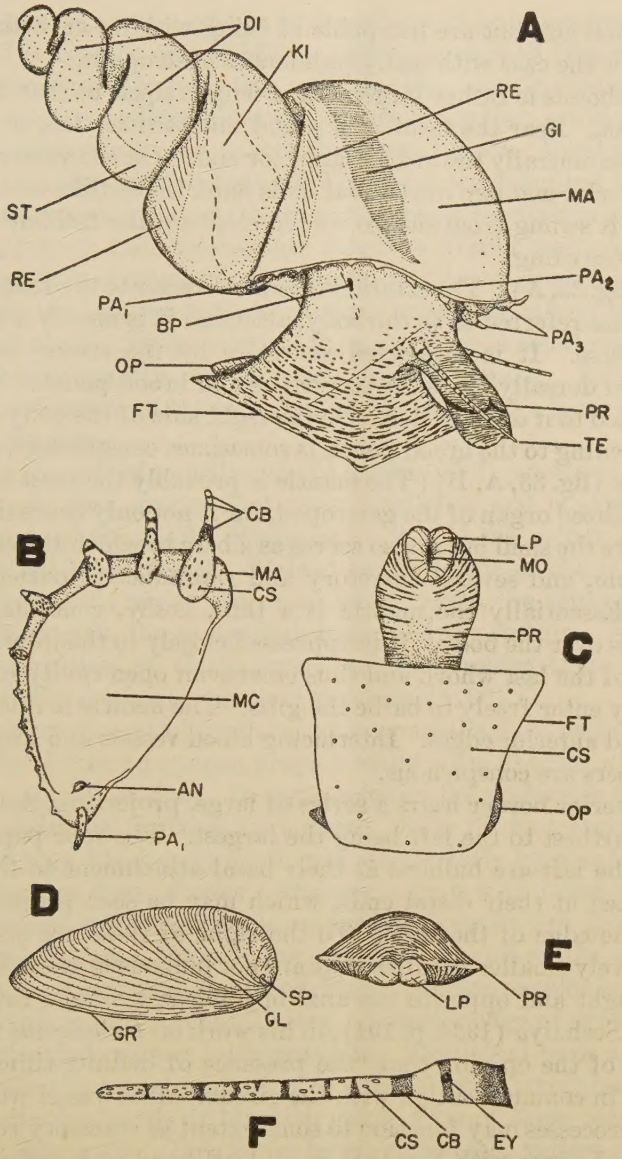


FIGURE 33.—EXTERNAL ANATOMY: **A,** Animal with shell removed to show areas of major organs (BP, birth pore; DI, digestive gland; FT, foot; GI, gills or ctenidium; KI, kidney; OP, operculum; $PA_1$, anal mantle papilla; $PA_2$, shell-forming edge of mantle; $PA_3$, mantle papillae; PR, proboscis; RE, intestine and rectum; ST, stomach; TE, tentacle). **B,** Edge of mantle looking into aperture with the body of the animal not shown (AN, anus; CB, grayish black color bands; CS, yellowish white color granules; MA, edge of mantle; MC, mantle cavity; $PA_1$, anal mantle papilla). **C,** View of underside of crawling animal (CS, yellowish color spots; FT, foot; LP, labial pads; MO, mouth; OP, operculum; PR, proboscis). **D,** Operculum, upper surface (GR, growth edge; GL, growth lines; SP, nucleus). **E,** Anterior view of proboscis (LP, labial pads; PR, carinate, lateral edge of proboscis). **F,** Dorsal view of right tentacle (CB, grayish black color bands; CS, yellowish color granules or spots; EY, eye).

their normal size but are incapable of being withdrawn within themselves, as is the case with many pulmonate gastropods.

The proboscis is rather large, with a length equal to that of the extended foot. Near the head it is round but becomes larger and flattened dorsoventrally toward the anterior end. On the ventral surface of the anterior end two oval labial pads flank the slitlike mouth. The proboscis is swung from side to side in elephantlike fashion when the animal is crawling.

Body (fig. 33, A) : The external region posterior to the foot and head is sometimes referred to as the body, although it is merely a continuation of these. It is supported ventrally by the strong columellar muscle and dorsally bears the esophagus and brood pouch. The mantle is welded to it on each side. On the right side of the body the small pitlike opening to the brood pouch is sometimes conspicuous.

Mantle (fig. 33, A, B) : The mantle is probably the most important and specialized organ of the gastropod, for it not only bears the glands that secrete the shell but it also serves as a base to which the ctenidium, osphradium, and several excretory and reproductive outlets are attached. Essentially the mantle is a thin, fleshy, cone-shaped cape that hangs over the body. It is appressed closely to the interior of the last half of the last whorl, and thus creates an open cavity into which water may enter freely to bathe the gills. The mantle is thicker at its lateral and anterior edges. Interlacing blood vessels and longitudinal muscle fibers are conspicuous.

The anterior border bears a series of large, projecting, fleshy papillae, the farthest to the left being the largest. The four papillae farthest to the left are bulbous at their basal attachment to the mantle and pointed at their distal ends, which may be seen projecting well beyond the edge of the shell. To the right of these are six to eight progressively smaller papillae that are not bulbous at their bases. To the far right and opposite the anal opening is a single, rather long, papilla. Seshaiya (1934, p. 191), in his work on *Paludomus tanschaurica*, was of the opinion that "the presence of definite sinuses in the processes in communication with the circumpallial vessel would show that the processes may function to some extent as accessory respiratory organs." I agree with him that in all likelihood such is the function of these papillae. It is significant to note that the largest ones are located on the left side where water flows into the mantle cavity. Seshaiya's contention that these papillae have little or nothing to do with the development of spiral sculpturing of the shell is further supported by the facts that: (1) The shell-producing area of the mantle is set posterior to the papillae, (2) there is no correlation between the position of the spiral rows of beads on the shell and that of the mantle papillae, and (3) *Hemisinus cubanianus* (Orbigny), from Cuba, bears papillae very similar to *Thiara*, yet its shell is smooth.

A comparative study of size and position of papillae was made in *Thiara* (*Plotiopsis*) *scabra* Müller, *Sermyla riquetii* Grateloup, and certain species of *Stenomelania*. While these mantle characters may be useful in generic determinations, it is felt that they are insufficiently distinct to separate species within the genus *Thiara*. Until now it was thought that the papillae-bearing Thiaridae were limited to the Old World, but examination of living specimens of *Hemisinus cubanianus* (Orbigny) from Cuba shows that this New World mollusk possesses mantle papillae very similar to those of *Thiara granifera*. The 7 papillae to the left are bulbous at their bases and extend beyond the edge of the shell. To the right of these are 13 to 14 small papillae. A solitary, long papilla to the far right is absent. Like *Thiara*, *Hemisinus* possesses a brood pouch on the back and a large birth pore on the right side.

Behind the row of papillae on the mantle of *T. granifera* there is a sharply impressed groove that runs parallel to and is superimposed on the edge of the shell. Posterior to this is the rather prominent circumpallial blood vessel. Welded to the inside of the mantle well within the mantle cavity are, from left to right, the osphradium, the ctenidium or gills, the urogenital ducts, and the rectum. A more detailed description of these organs is given under their respective systems, in the section on internal anatomy (p. 90).

Color of animal: Color of animal in general a dark yellowish gray. Underside of foot an opaque grayish white with 10 to 20 widely scattered, round, yellow dots. In some colonies the underside of the foot has an additional pinkish undertone. Side of foot speckled with clumps of tiny, black-gray spots, which anteriorly become thin, short, black irregular lines of color. Proboscis gray with transverse black, fine striations, which are more prominent dorsally but disappear on the ventral surface. Toward the anterior end and on the dorsal side is a prominent, inverted, V-shaped, black, transverse color band, which is characteristic of the genus *Thiara*. Anterior edge of proboscis with small, embedded, yellow color-granules. The labial pads are pinkish gray. Tentacles translucent gray to colorless with irregularly spaced, narrow, circular bands of blackish gray. One of these bands crosses the small, black eye. Relatively large, embedded, yellow color-spots are often present in the tentacle. The mantle papillae are colored similarly to the tentacles. Inside of mantle a brilliant copper-green. Birth pore usually tinted with pink.

## INTERNAL ANATOMY

A general orientation is presented here as an aid to parasitologists who may wish to examine snails that have been experimentally infected with larval trematodes. In most instances only the digestive gland

956649—52——2

need be removed for gross examination or sectioning, but occasion may demand search in other organs in studies concerning the migratory paths of entering miricidia or escaping cercariae. Attention is drawn to the section on parasitology (p. 108).

The animal is held within in its protective shell by the strong, curved columellar muscle running posteriorly from the opercular region of the foot and curving around the inner columella. In material that has been preserved in formalin or 70 percent alcohol the columellar muscle loses its strength of attachment to the shell, and animals are usually easily drawn from their shell with the aid of a bent pin or sharp, curved probe. It is impossible to extract the animal of living specimens without seriously rupturing most of the organs. The shell must be cracked and picked away from the region of the penultimate whorl (the whorl above the aperture) to expose the area where the muscle is attached to the columella. A dissecting pin may be used to scrape away the attaching fibers. Living material has the additional disadvantage of becoming sticky from the exudation of mucus. However, certain organs are more easily found and studied in fresh material than in preserved specimens.

The general position of organs is shown in figure 33, A. The most conspicuous and most easily found organ is the "liver," or digestive gland, which in preserved material is a sandy brown and in fresh material is darkish green with numerous, small, embedded black spots. The digestive gland usually occupies the apical or top two or three whorls. Embedded in the columellar side or inside of the coil is the small, tubular-shaped gonad. Just below the digestive gland is found the rather large stomach, which may be easily found by tracing back along the easily seen feces-packed intestine. Between the stomach and the lower part of the intestine may be found the oval-shaped, sac-like kidney, which is conspicuous in its possession of internal fleshy septa or lamellae. Lying beside the kidney, and also just anterior to the stomach, is the pericardial sac, which contains the single auricle and one ventricle. The position of the heart may also be found by following back along the ctenidium, which arises at the base of the auricle. The esophagus is usually thin walled, small, and difficult to find at first, but may be more easily located at the point of its juncture with the posterior end of the stomach or where it emerges from between the brood pouch and the columellar muscle.

### ALIMENTARY SYSTEM

FIGURES 34–36

PHARYNGEAL REGION: The mouth is a vertical, narrow slit located at the anterior end of the proboscis. It and the two labial pads that flank it on either side face slightly ventrally. The oral

cavity is relatively short and round, although in preserved and shrunken material it is apt to become folded. Two ovoid, horny jaws are located on each side of the posterior region of the oral cavity. They are hinged together at their dorsal edges by a thin, transparent, hyaline sheath, which extends beyond the edges of the jaws slightly laterally and posteriorly. The anterior edge of these brown jaws is serrate. Small, polygonal platelets make up the anterior half of each jaw. The posterior region from which these platelets arise and are pushed forward is translucent-gray and smooth.

Just posterior to the jaws is found the large, bulbous buccal mass, which contains the radula ribbon and the two salivary glands. If the dorsal surface of the proboscis is slit open, the buccal mass is readily observed. Within the various muscles and ventral to the buccal cavity are found two pinkish, ovoid, translucent buccal cartilages. They are connected dorsally by a transverse muscle. Tensor superior muscles rise from the dorsolateral surfaces of the cartilages and run forward and inward to attach themselves to the hyaline sheath or elastic membrane of the radula ribbon. A number of other muscles, which aid in the manipulation of the radula, are present.

The salivary glands are two serpentine, thin-walled tubes, which enter the buccal mass slightly to either side of the median line on the dorsal surface. The glands coil posteriorly closely appressed to the esophagus as far back as the central ganglia of the brain. The number and nature of these glands is similar to those found in *Paludomus* (Seshaiya, 1934) and the Amnicolidae. Riech's (1937) observations on *Thiara scabra*, in which a dozen or so short salivary glands were noted, are not in conformity with what has been found in other gastropods in these families.

The radula ribbon, which the animal rolls back and forth to rasp at its food, is set in the center of the buccal mass. Its more highly developed anterior end lies exposed on the bottom of the buccal cavity. Posteriorly, where yet unused teeth are curled tightly together within a protecting tubular sheath, the radula descends through the buccal floor, runs slightly anterior within the buccal mass, and then turns posteriorly once more to leave the buccal mass. This free end is the swollen, rudimentary region where new teeth are being continually formed and pushed forward. Underlying the anterior section of the radula is a broad, winged hyaline sheath or elastic membrane, which on its dorsal side serves as anchorage for the individual teeth, and which on its ventral and lateral sides serves as a connecting base for muscles.

The radula is of the taenioglossate type, with the number of rows from rudiment to leading edge varying in adults from 60 to 115, although 85 to 95 appear most frequently. Each transverse row consists of 7 teeth. In the center is the smallest, the central or rachidian

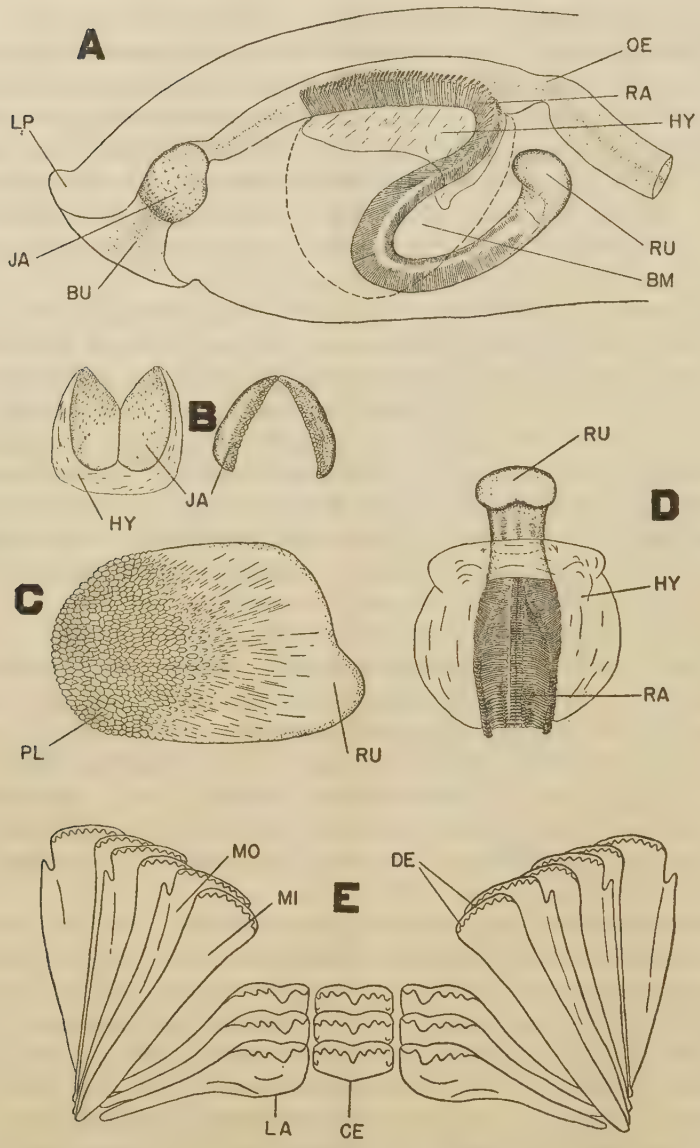


FIGURE 34.—PROBOSCIS AND ITS PARTS: **A,** Sagittal section (semidiagrammatic) of proboscis (BM, dotted line showing limits of buccal muscle and cartilage; BU, oral cavity; HY, hyaline sheath or basal membrane of radula; JA, left jaw; LP, labial pads; OE, esophagus; RA, radula or odontophore; RU, rudiment of radula). **B,** Dorsal (left) and anterior (right) view of paired jaws (HY, hyaline sheath; JA, jaws). **C,** Outer view of right jaw (PL, platelets; RU, rudiment of jaw). **D,** Dorsal view of exposed radula (HY, hyaline sheath or basal membrane; RA, teeth of radula; RU, rudiment). **E,** Three rows of radula teeth in their natural position (CE, central or rachidian tooth; DE, denticles found on leading edge of all teeth; LA, lateral tooth; MI, inner marginal; MO, outer marginal).

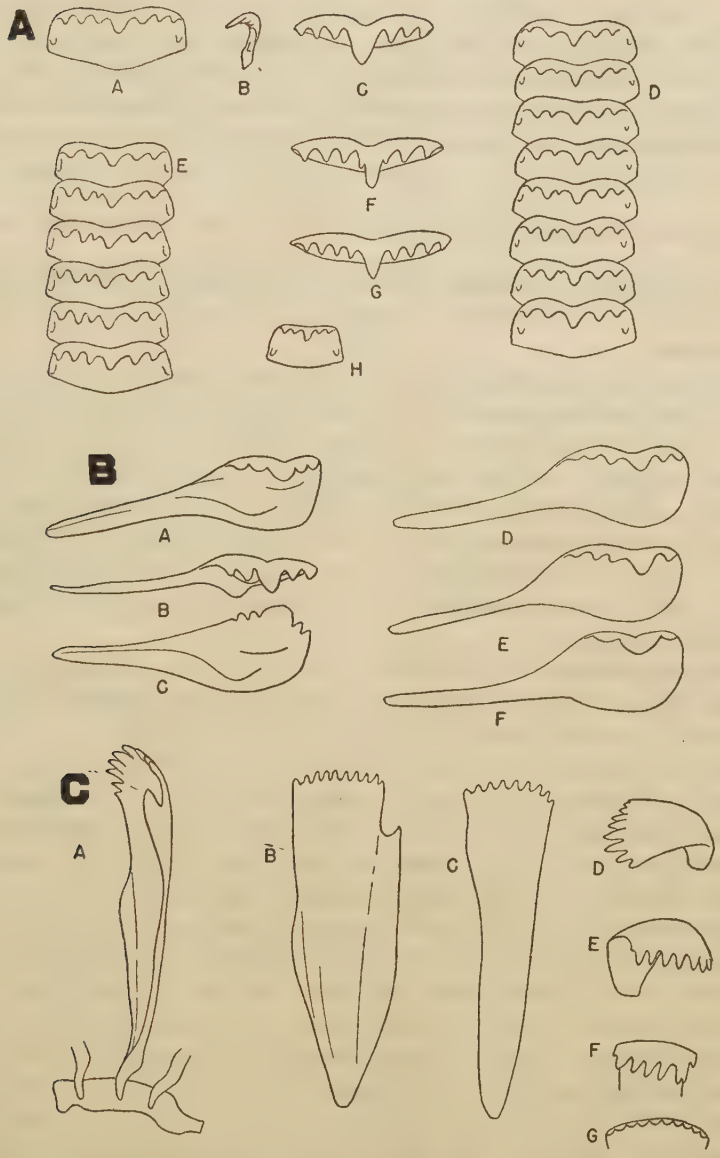


FIGURE 35.—DETAILS OF RADULA: **A,** Central teeth (A, anterior view; B, lateral view; C, dorsal view; D, row of 8 centrals showing variation in number of denticles; E, row of 6 centrals showing similar variation; F, G, dorsal view, showing denticle variation; H, central of young snail removed from parent's brood pouch, showing prominence of the two basal denticles in each lower corner). **B,** Lateral teeth (A, C to F, anterior view of 5 different laterals; B, dorsal view of lateral). **C,** Marginal teeth (A, side view of outer marginal, showing attachment to basal membrane; B, outer marginal; C, inner marginal; D to G, dorsal view of inner marginals, showing variations in number of denticles).

tooth. On each side of this is a larger lateral tooth. Two more pairs flank the laterals, first the inner marginals, and, lastly, the outer marginals. On the top and leading edge of each tooth are many small, pointed denticles that face anteriorly. These denticles are often used for identification purposes and are generally designated by numbers in malacological works. Hence the formula for the central tooth (fig. 34, E:CE) is $\frac{3\text{–}1\text{–}3}{1\text{–}1}$, indicating that the leading edge bears 1 large denticle in the center with 3 smaller ones on each side. Below these is a pair of basals, one situated at each bottom and outer corner of the tooth.

The teeth are transparent and of the consistency of very stiff rubber. They are best observed in water between a slide and coverslip. Staining by various conventional means does not appear to bring out any more detail, and, to the contrary, often obscures certain delicate features. Water mounts have the additional advantage of permitting a maximum of manipulation in which the teeth may be further separated, rolled, or flattened at will by nudging the coverslip back and forth. When dried, the radula may be covered with euparol and the coverslip replaced.

Observations on the radula and the illustrations in figures 34 and 35 are from a colony from Naujan River, Mindoro Island, Philippine Islands, P. Bartsch collector (U.S.N.M. No. 258890).

The central tooth is oblong and slightly more than twice as wide as high. The usual count on the leading edge is 3–1–3, although 2–1–2 is not uncommon. This variation may occur within one ribbon and appears to arise from the changing nature of the cells that form these teeth. Figure 35, A : E, shows a group of centrals, which anteriorly have a count of 3–1–2, but which progressively reduce the size of the extra denticle on the right side, until 5 teeth posterior to this the count becomes 2–1–2. Examples of additions of denticles were also noted. The maximum number of denticles seen was 4–1–4 but was noted only on one occasion. Not previously noted, and probably overlooked by other workers, are two small basals which are most prominent in centrals of very young individuals (fig. 35, A : H). In older specimens these basal denticles are formed nearer the sides and closer to the leading edge and likely have been misinterpreted as being abnormally placed denticles of the leading edge.

The lateral tooth is asymmetrical with the denticle-bearing oval section closest to the central. Lateral to this is the armlike extension, which is attached to the hyaline sheath. The denticle count is most frequently 1–1–2, quite often 2–1–2, and rarely 2–1–3. The counts appear to be more stable throughout the ribbon than is the case in the central, but occasionally the left lateral may differ consistently from the right lateral in the same animal.

The marginals are slightly spatulate and very similar in appearance. The inner marginal is always slightly shorter and narrower than the outer marginal. There is considerable variation in the number of denticles, with the counts of each often overlapping the other. The inner marginal has been observed to bear 9, 8, or 7 denticles, the outer marginal 12, 11, 10, or 9. The most important feature of the outer marginal is a small, sharp, thumblike protrusion on its outer edge. This feature has not been previously recorded in the literature, and has also been found by the author in other members of the Thiaridae. It is easily overlooked, and usually requires fresh material, which is observable in water mounts.

Esophagus: The thin-walled, rather narrow esophagus dips ventrally upon leaving the buccal mass and then passes through the brain, with the central ganglia dorsal to it, the pedal ganglia below, and the cerebro-pedal commissures on each side. It travels in a straight line posteriorly along the underside of the large brood pouch and emerges, with a slight twist to the right, over the end of the columellar muscle. It then passes up past the lower stomach and joins the posterior or upper stomach at its posterior and ventral end.

Stomach: The stomach is a rather large sac located in about the second-to-the-last whorl and is bounded posteriorly by the large digestive gland and anteriorly by the heart and kidney. The stomach has a circular constriction at its center, which divides the lower stomach or crystalline sac from the upper stomach proper.

The esophagus enters the stomach at one corner at the posterior end. Below the esophageal entrance is a large, grooved, central mass, or core. The remainder of the sides of the stomach are lined with 40 to 50 raised, transverse lamellae or platelets. At the bottom of the stomach on the side opposite the central core is the small, circular opening from the crystalline style sac. The food passes slowly down the stomach, across this entrance and over to the corner, where it exits into the intestine.

The crystalline style sac is essentially a diverticulum of the stomach proper. It often appears as a transparent sac in fresh material. Within its thin walls is a round, folded hyaline sheath, iridescent, and open at its posterior end, which faces the stomach. Within this is the crystalline style itself, shaped like a dumbbell and jellylike in consistency.

Two rather large openings are present not far from the esophageal opening at the posterior end of the stomach proper, which constitute the connection with the hepatopancreas, or digestive gland. The top, or spire whorls, of the animal contain the digestive gland, which anteriorly partially enwraps the upper stomach.

Intestine: The intestine is thick walled, fairly large, and round. It passes downward in close contact with the crystalline style sac, on

the outer surface of which it forms an S-shaped coil. Beyond this the intestine becomes thin walled and transparent. The long, round feces become packed in oblique rows as they pass toward the anus. The last section of the intestine is welded to the right side of the mantle. When feces pass from the small, round anus, they usually drop down the right side of the body. Their passing is facilitated by a shallow, ciliated groove, running from the region of the birth pore obliquely forward and downward toward the edge of the foot.

### NERVOUS SYSTEM

FIGURE 37

The central ganglia of the nervous system are concentrated in the head region a little behind the proboscis. They may be reached easily by slitting open the dorsal side of the proboscis and head. The esophagus runs directly through the group, as described previously. The brood pouch borders the posterior regions of these ganglia remarkably closely, and on more than one occasion young snails have been found within 0.5 mm. of the central ganglia. The two large pedal ganglia are more difficult to reach, for they are set deeply in the fore regions of the foot directly below the other ganglia.

The central ganglia have a thick dorsal covering of connective tissue. The surfaces of these ganglia are colored a deep maroon in living specimens. In preserved material the color is waxy white. They are oval, with thicker and more rounded posterior ends, and with tapering, dorsoventrally flattened anterior ends, which give rise to six small nerves. The two ganglia are united by a very short, thick commissure. The number and size of the anterior nerves may vary, although the more important ocular and tentacular nerves, which are the most laterally placed, are constant. The inner four or five nerves run

---

FIGURE 36.—ALIMENTARY SYSTEM: **A,** Dorsal view of buccal mass (semidiagrammatic) (BS, buccal sac; LC, left central ganglion; MO, mouth; OE, esophagus; RM, retractor muscle; SG, salivary gland). **B,** Sagittal section of esophagus (MO, mouth; OE, esophagus; SG, left salivary gland). **C,** Crystalline style; top figure from preserved specimen; bottom figure from life. **D,** Semidiagrammatic view of entire alimentary system (AN, anus; DD, digestive ducts coming from digestive gland; FE, feces in intestine; IN, intestine; OE, esophagus; RE, rectum or lower intestine; SS, lower stomach or crystalline style sac; ST, stomach). **E,** Dorsal view of esophagus as it passes posteriorly from beneath the edge of the brood pouch (LM, longitudinal muscles; OE, esophagus); PO, brood pouch. **F,** Left lateral view of stomach (IN, intestine; OE, esophagus; SS, crystalline style sac; ST, upper stomach). **G,** Interior of stomach; top left and bottom left, cross-sections; right figure, longitudinal section (CC, central column; CS, entrance of crystalline style sac; DD, ducts to and from digestive gland; HY, hyaline sheath surrounding style; IN, intestine; OE, esophagus; OS, outer wall of crystalline style sac; PL, plicae of stomach wall; SL, lumen of stomach).

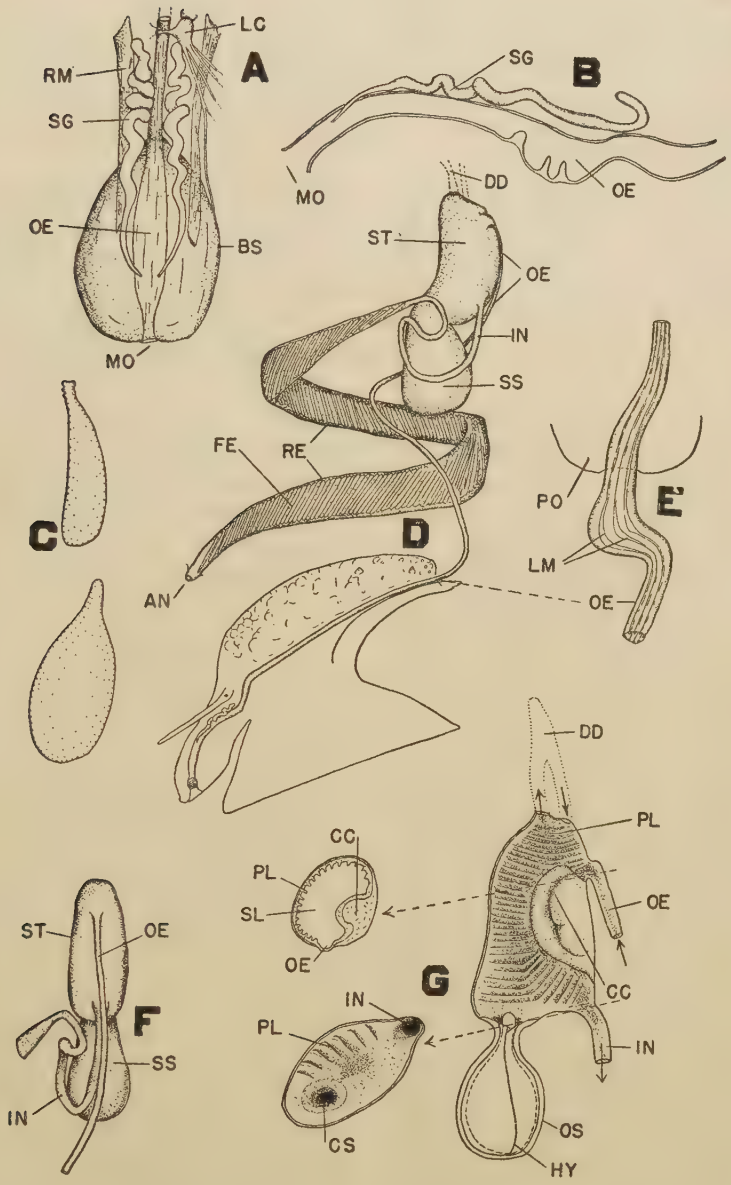


FIGURE 36.—(See opposite page for legend.)

956649—52——3

anteriorly to supply the proboscis, the labial region, and the muscular elements of the buccal mass. The innermost nerve runs to the anterior region of the buccal mass, turns posteriorly, and runs back to join the buccal ganglia at the posterior end of the buccal mass.

Each cerebral ganglion gives rise ventrally to a stout commissure, which descends to the pedal ganglion below it. At a point on the pedal ganglion, just posterior to the entrance of the cerebro-pedal commissure, another large commissure enters from the pleural ganglion.

The pedal ganglia are larger than the cerebral ganglia and, in *Thiara*, are strikingly different from those in the Amnicolidae in being laterally rather than dorsoventrally compressed. They are closely connected at their inner surfaces and do not have what might be called a commissure. The ventral ends of these ganglia each give rise to two stout pedal nerves. Smaller offshoots of varying size may be present.

The statocysts are rather prominent in this species and are located on the upper ventral surface of each pedal ganglion. No prominent nerve running from the statocyst to the cerebral ganglion was observed, although there is one in *Paludomus* (Seshaiya, 1934), *Thiara* (*Thiara*) *amarula*, *Thiara* (*Melanoides*) *tuberculata*, and *Thiara* (*Melanoides*) *costata* (Bouvier, 1887). However, a rather prominent nerve is found descending ventrally from the statocyst. Each statocyst contains a single calcareous, disc-shaped statolith or otolith. Other members of the genus *Thiara* possess a similar otolith, but those of *Paludomus* (Seshaiya, 1934), *Nassopsis*, and *Bythoceros* (Moore, 1889) contain numerous small otocones.

The pleural ganglia are round and bulbous and closely appressed to the ventral and posterior end of the cerebral ganglia. They are connected to the latter by short commissures. The right pleural ganglion gives rise to the rather large supraintestinal nerve and the right pallial nerve. The former nerve joins the small supraintestinal ganglion on the left side of the body. The left pleural ganglion gives off on its left side a small nerve, which passes up to the left side of the mantle region. Just behind this ganglion is the equally large, oval, subintestinal ganglion. At its juncture with the pleural ganglion another thin nerve arises to the left and ascends toward the mantle.

The posterior end of the subintestinal ganglion gives rise to two prominent nerves: (1) A pallial nerve, which first makes a short, complete loop and then passes across the back of the animal to the right side, where it is joined by a similar nerve from the right pleural ganglion; and (2) the right visceral nerve, which proceeds posteriorly to join the small obscure visceral ganglion.

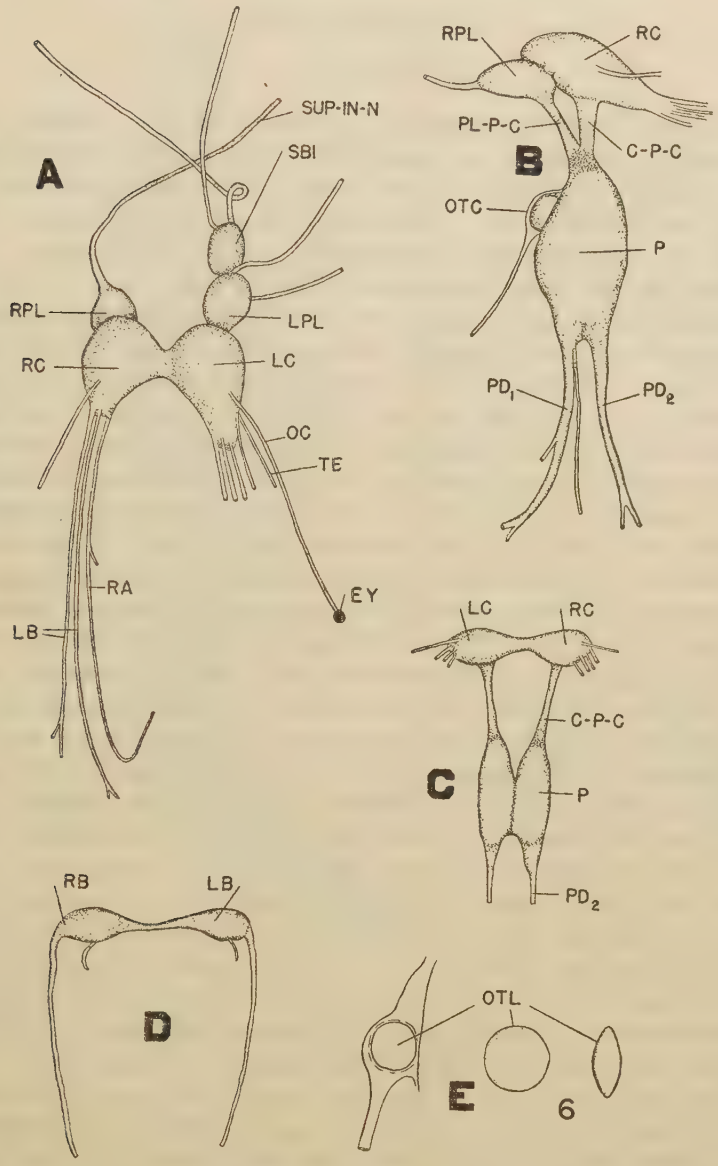


FIGURE 37.—CENTRAL NERVOUS SYSTEM: **A,** Dorsal view of central ganglia and its nerves (EY, eye; LB, labial nerves; LC, left cerebral ganglion; LPL, left pleural ganglion; OC, ocular nerve; RA, nerve to region of radula; RC, right cerebral ganglion; RPL, right pleural ganglion; SBI, subintestinal ganglion; SUP–IN–N, supraintestinal nerve; TE, tentacular nerve). **B,** Right lateral view of central ganglia (C–P–C, cerebro-pedal connective; OTC, otocyst; P, pedal ganglion; $PD_1$, posterior pedal nerve; $PD_2$, anterior pedal nerve; PL–P–C, pleuro-pedal connective; RC, right cerebral ganglion; RPL, right pleural ganglion). **C,** Anterior view of central ganglia (C–P–C, cerebro-pedal connective; LC, left cerebral ganglion; P, pedal ganglion; $PD_2$, anterior pedal nerve; RC, right cerebral ganglion). **D,** Dorsal view of left (LB) and right (RB) buccal ganglia. **E,** Otocyst and otolith (OTL).

CIRCULATORY SYSTEM

FIGURE 38

The small saclike pericardium is situated at the posterior end of the ctenidium in the region between the kidney and the lower stomach, or crystalline style sac. There is one auricle and posterior to it a single, smaller ventricle. The auricle is round and bulbous, with thin walls. In preserved material, "jellied" blood fills this organ. At its anterior end the large, efferent ctenidial vessel enters. At its posterior end it joins the ventricle. The ventricle is somewhat triangular with its broad base appressed to the auricle. It is relatively thick walled with a large number of separate, long muscle fibers running crisscross over the inner surface. Many of these fibers join at the anterior end to form a round valve, which prevents blood from reversing its course. On the ventral surface at the apical end of the ventricle there is another slitlike valve. At this point the blood enters the thin-walled transparent truncus arteriosus, which soon divides into an anterior and a posterior, or visceral, artery. The latter is round in cross-section in living material but collapses in preserved specimens. It runs posteriorly, first giving off a short artery to the left, which supplies the region of the crystalline style sac. It proceeds farther toward the apical whorls in close proximity to the stomach and then proceeds anteriorly to supply the anterior region of the foot and body.

The venous system has not been followed adequately in this species because of the difficulties in following the numerous sinuses. It appears that the sinuses that bathe the various organs are ill defined and have complex interconnections. The rectal sinus is the most easily found, and it is situated in the region of the lower part of the kidney and the intestine. The blood flows from this largest sinus into the ctenidial lamellae. Small sinuses have been noted in the region of the pedal ganglia, digestive gland, esophagus, and stomach. The complex of sinuses noted in the mantle of *Paludomus* by Seshaiya (1934) are similar, but are more highly developed than in *Thiara granifera*.

The bluish-green color of the mantle and other parts of the internal organs noted by Seshaiya (1934) is common not only to *Paludomus* and *Thiara* but also to a number of New World members of the Thiaridae. Seshaiya suggests that this is due to the presence of haemocyanin in the blood.

The ctenidium is long and narrow and is welded to the mantle. It extends from the apex of the mantle cavity in the region of the heart forward almost to the mantle edge. It bears approximately 190 to 200 separate gill lamellae, which are triangular, and which hang with their apices facing downward into the mantle cavity.

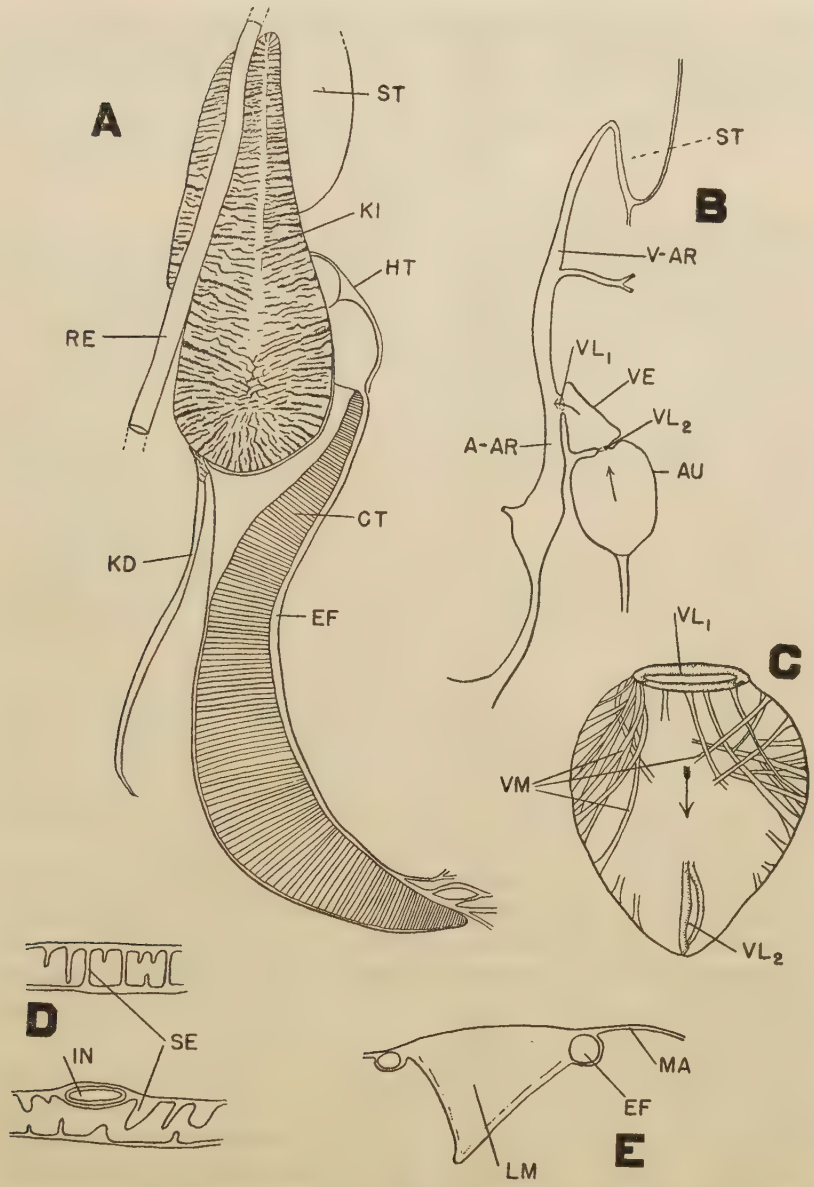


FIGURE 38.—EXCRETORY, CIRCULATORY, AND RESPIRATORY SYSTEMS: **A,** Kidney and ctenidium (CT, ctenidium or gills; EF, efferent vein from gills to heart; HT, pericardial sac containing auricle and ventricle; KD, kidney duct; KI, kidney; RE, rectum; ST, stomach). **B,** Heart (A-AR, anterior artery; AU, auricle; ST, stomach; V-AR, visceral artery; VE, ventricle; $VL_1$, posterior ventricular valve; $VL_2$, anterior ventricular valve). **C,** Dorsal view of heart (semidiagrammatic) showing the network of heart muscles (VM), the anterior ventricular valve ($VL_1$), and the posterior ventricular valve ($VL_2$). **D,** Cross-sectional views of kidney showing the septa (SE) and the embedded intestine (IN). **E,** Side view of a gill lamella (LM) attached to the mantle (MA) and showing the efferent artery (EF).

To the left of the ctenidium, and about half its length, is the narrow, tubular osphradium or "organ of smell." It is also closely welded to the mantle.

### UROGENITAL SYSTEM

FIGURES 38, 39

KIDNEY: The renal organ is a rather large, easily seen, oval sac lying in the region between the stomach and the apex of the mantle cavity. At its posterior end, where it borders the right side of the crystalline style sac, it is narrow, but widens and flattens toward its anterior end. The intestine is partially encased by the right side of the kidney. Internally the kidney is made up of a network of thin lamellae or septa, between which are the blood spaces. The lamellae are arranged in a more or less regular pattern and all pointing toward the center of the kidney. This pattern is easily seen through the thin outer wall of the organ. No prominent renal aperture leading into the mantle cavity could be found. An obscure renal duct could be followed in a few specimens, which led down the right, lower side of the kidney and passed along the mantle wall to an exodus beside the genital orifice.

GONADS: The gonads in this species are small and lie on the inside of the whorls of the digestive gland in the spire. In living material they consist of a bright yellow tubule, which gives off numerous smaller branches. Eggs were observed by crushing small portions of the gonads on a slide. No sperm were observed in either living material or in histological sections made from preserved material.

The genital orifice is surrounded by a small, elongate, cup-shaped flap, the opening of which faces the entrance of the brood pouch a few millimeters away. Eggs have not been observed passing from the oviduct to the brood pouch, but it is possible that the flap of the genital orifice is pressed against the pouch entrance when the animal is completely withdrawn into its shell.

The brood pouch is not developed until the animal begins to reach maturity. In its early formation the pouch consists of an irregular, flattened hollow in the connective tissue of the back of the animal. As more eggs are added and the hatched young grow, the pouch is enlarged and becomes irregularly divided into small compartments. Thin, transparent walls of adventitious tissue separate the various groups of young, but all stages of development of the young may be represented in these compartments. The more advanced young either push or eat their way through these thin walls to other compartments. In a highly developed pouch the dorsal wall is thin enough to reveal the young crawling about inside. The pouch may extend from the region immediately behind the tentacles and central ganglia posteriorly

to the very apex of the mantle cavity. Below it are the esophagus and the foot and columellar muscles. In one colony (Naujan, Mindoro Island, Philippine Islands) it was not uncommon to find in the more highly developed pouches an auxiliary pouch extending down the right side of the body below the right tentacle.

TABLE 2.—*Contents of brood pouches*

SPECIMEN No. 1

| Number of young | Length of shell (mm.) | Number of whorls |
|---|---|---|
| 1 | 1. 9 | 4. 5 |
| 1 | 1. 8 | 4. 2 |
| 2 | 1. 0 | 3. 8 |
| 2 | . 8 | 3. 8 |
| 1 | . 7 | 2. 8 |
| 1 | . 5 | 2. 7 |
| 2 | . 3 | 2. 1 |
| 2 | . 2 | 1. 6 |
| 12 | . 1 | 1. 2+ |
| 25 | (Less than 1 whorl) | --- |
| 50 (Eggs) | --- | --- |

SPECIMEN No. 2

| | | |
|---|---|---|
| 1 | 2. 2 | 4. 5 |
| 1 | 1. 8 | 4. 3 |
| 1 | 1. 6 | 4. 0 |
| 1 | 1. 4 | 3. 5 |
| 1 | 1. 2 | 4. 0 |
| 2 | . 9 | 3. 0 |
| 1 | . 5 | 2. 5 |
| 2 | . 2 | 2. 0 |
| 5 | (Less than 1 whorl) | --- |
| 0 (Eggs) | --- | --- |

SPECIMEN No. 3

| | | |
|---|---|---|
| 1 | 1. 8 | 4. 8 |
| 1 | 1. 5 | 4. 5 |
| 1 | 1. 2 | 3. 5 |
| 1 | 1. 0 | 4. 0 |
| 6 | . 9 | 3. 5 |
| 9 | . 7 | 3. 0 |
| 5 | . 2 | 2. 0 |
| 30 | . 1 | 1. 5 |
| 20 | (Less than 1 whorl) | --- |
| 50 (Eggs) | --- | --- |

Young emerge from the pouch on the right side through the birth pore, which also serves as the egg entrance. The pore is bordered by a small, raised fleshy ridge. Young have been observed emerging spire first in living specimens (Agaña Spring Colony, Guam Island, Marianas). There appears to be no special order or time for leaving the pouch, and young of varying sizes have been observed being born

from the same mother. In fresh specimens from Guam, numerous, irregularly shaped calcium-carbonate grains about 0.2 mm. in diameter have been found. It is possible that developing young feed on these concretions. Occasionally a young snail may fail to escape from the pouch, and in these cases no other young or eggs are found in the pouch. These giants often grow to one-fifth the size of the mother and probably rupture through the dorsal wall or cause the death of the parent.

Guam specimens kept in small vials of water gave birth to one young on an average of every 12 hours. Three mature individuals were dissected (Agaña Spring), with the brood pouch contents noted as in table 2.

*Reproduction in related groups.*—The family Thiaridae exhibits an interesting series of modifications within certain genera with regard to manner of reproduction. It is believed that the more primitive types are derivatives of the marine family Cerithiidae, a very similar group in shell, radula, and animal characters. A number of Cerithiidae are estuarine in habitat, and like their truly marine representatives possess a veliger larval phase. Seshaiya (1940) has made the remarkable discovery of a veliger stage in the fresh-water thiarid *Stenomelania crenulata* Deshayes, in India. He found that the breeding season commences about November and extends until the following April. During this period the brood pouch on the back of the animal contains thousands of developing eggs and a few veligers just escaped from the vitelline membrane, but no juvenile, shelled forms. The veliger stage, of about 2 weeks' duration, is spent in active swimming in the river water. The full-grown veliger has the typical form found in the life history of many marine gastropods and has two veliger lobes provided with long cilia, by means of which it propels itself. Seshaiya also noted the curious phenomenon found in many marine invertebrates, that of spawning on the day previous to the full moon and for the two succeeding days.

A more advanced type of brooding of young within a neck pouch is found in *Thiara* and *Brotia*. In the former there are fewer and much larger-shelled young retained for a number of weeks within the pouch.

A still more curious brooding modification is found in some other thiarids such as *Semisulcospira*, of Japan, and the African (Lake Tanganyika) genera *Tiphobia*, *Tanganyicia*, and *Nassopsis* (Moore, 1898). Brooding takes place in the enlarged oviduct, which is welded to the mantle. In the case of *Semisulcospira* the shelled young are rather small and all of the same size. Spermatozoa have been observed in male specimens.

The habit of laying eggs rather than brooding is considered to be a more nearly perfect adaptation to fresh-water conditions. *Paludomus*, of Ceylon, India, the Philippine Islands, and southern

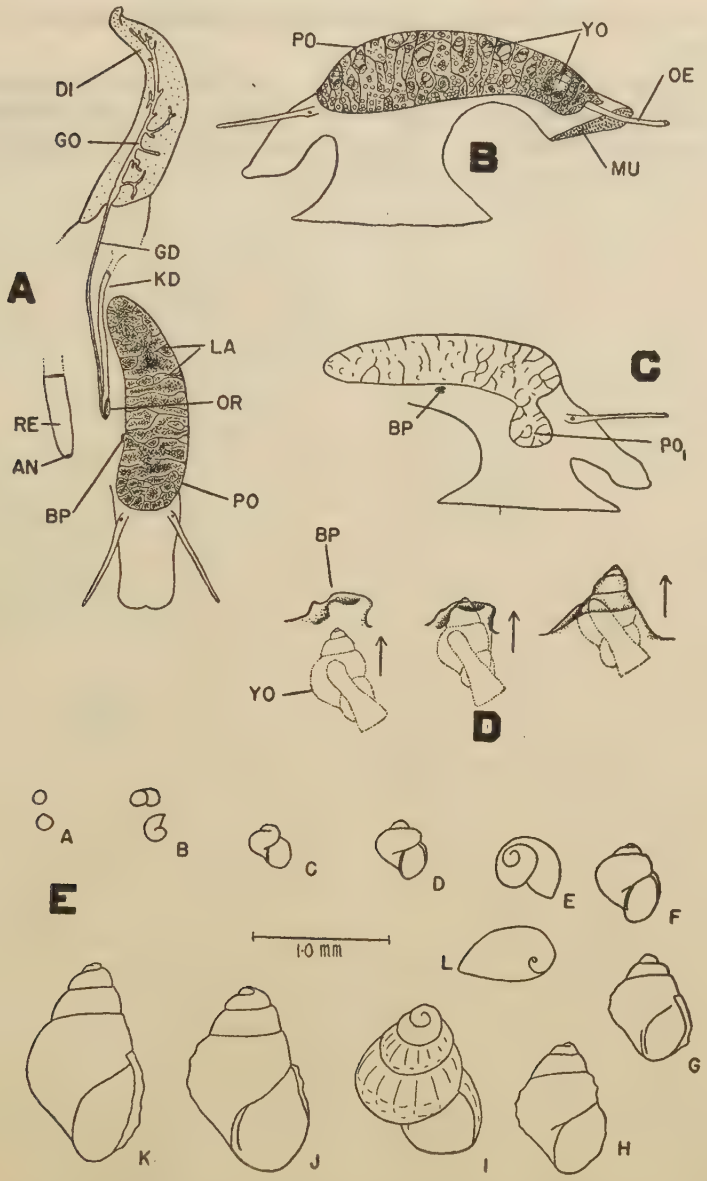


FIGURE 39.—REPRODUCTIVE SYSTEM: **A,** Dorsal view of reproductive system (semidiagrammatic) (AN, anus; BP, birth pore; DI, digestive gland; GD, gonoduct; GO, gonads; KD, kidney duct; LA, lamellae of adventitious tissue; OR, genital orifice; PO, brood pouch; RE, rectum). **B,** Side view of animal, showing young in brood pouch (MU, columellar muscle; OE, esophagus; PO, brood pouch; YO, young.) **C,** Side view of animal, showing abnormal extension ($PO_1$) of brood pouch on right side. **D,** Birth pores (BP), showing living young (YO) emerging. **E,** Selected individuals from brood pouch, showing development from egg (A) to young with four whorls (K) (sculpturing has been drawn only in figure I); (L, operculum of brood-pouch young).

China, and the several American genera of Pleurocerinae are among this type.

A completed study of the various reproductive modifications in this family on a world-wide basis should reveal a very interesting evolutionary pattern and should aid in solving many of the present phylogenetic problems in this group.

FIGURE 40.—Map of southern Guam Island, showing collecting localities and relative mean shell-size of colonies (see p. 103 for explanation).

## LIFE HISTORY

### HABITAT

As has been stated earlier, the various subspecies or geographical races of *Thiara granifera* have not been studied adequately, so that details of its geographical distribution cannot be presented at this time. However, the limits of its distribution as a whole are fairly well known. This species lives in fast-flowing fresh-water streams. Its most westerly limits include the Island of Ceylon and the eastern coast of India. Its range extends easterly to include the coasts of Siam and southern China, the East Indies, and the Philippine Islands. To the north it is found on Formosa (Taiwan) Island and the small islands south of Japan. Farther east, it is common in Melanesia, especially the Solomon Island Archipelago, the Marianas, and the Polynesian islands of the Hawaiian and the Society Islands. Undoubtedly the topography and nature of the areas in which this species is found varies from place to place, but it is highly likely that certain optimum environmental conditions are common to all its localities. Thus we may find this species in streams very near the sea in certain small islands, but considerably inland and at higher altitudes on such large islands as Luzon, Leyte, and Mindanao in the Philippine Islands.

In the isolated Micronesian islands of the Marianas only three islands are large enough to have permanent streams: Guam, Saipan, and Rota. All three support colonies of *Thiara* (*Plotiopsis*) *scabra*, but only the first possesses streams large enough to maintain populations of *Thiara* (*Tarebia*) *granifera*. Guam (Guajan) Island is 32 miles long by 4 to 10 miles wide and about 225 square miles in area. It is mountainous in the southern half, where a great number of small streams flow down to the sea. The northern half forms a low plateau, which is devoid of permanent streams.

The majority of the streams in the southern half of Guam are colonized by *Thiara granifera*. Collections were made at the localities listed. The number following each station record indicates the number of specimens collected (fig. 40).

A. Zadue Maagos River. 1945. D. Frey collector. 92.

B. Agaña Spring, 1½ miles southeast of Agaña. April 22, 1945. R. T. Abbott collector. 198.

C. Talisai stream, under bridge, 2 miles southeast of Agat. May 1, 1945. R. T. Abbott collector. 100.

D. Water Plant, 2 miles up Ylig River. April 26, 1945. R. T. Abbott collector. 65. Flow rapid, 6 feet wide, 6 inches deep.

E. 1 mile up Pago River. April 26, 1945. R. T. Abbott collector. 50. Flow rapid, 6 feet wide, 4 inches deep.

F. First stream 600 yards south of Piti. April 24, 1945. R. T. Abbott collector. 38. Flow sluggish, 3 feet wide, 1 inch deep; shady.

G. Geus River. 1945. D. Frey collector. 97.

H. 100 yards up Aguada Stream. April 24, 1945. R. T. Abbott collector. 127. Flow sluggish, 4 feet wide, 2 inches deep; shady.

I. 1 mile up La Sa Fua River. May 10, 1945. R. T. Abbott collector. 20. Flow sluggish, 4 feet wide, 2 inches deep; shady.
J. ½ mile up Inarajan River. May 2, 1945. R. T. Abbott collector. 43.
K. Merizo River. 1945. D. Frey collector. 245.
L. Small stream near Ajino Beach. 1945. D. Frey collector. 8.
M. ½ mile up Umatac River. May 10, 1945. R. T. Abbott collector. 36. Flow rapid. 30 feet wide, 8 inches deep; no shade.

The snails are most abundant in the shallow riffles where the flow of water is fairly rapid and where the bottom consists of a pavement of small stones. Occasionally the snails may be found congregated on firm sandy bottom provided there is a healthy flow of water. Waters of the stream that are exposed to direct sunlight during most of the day appear to attract this species. The upper reaches of the streams that have a very rapid flow of water are not favorable, although other mollusks such as *Neritina* and *Septaria* may be abundantly represented. The tiny flows of headwater tributaries, which are less than a foot in width and 2 inches in depth, will not support *T. granifera* but are favorable to *T. scabra*. The stream at Umatac, in the southwest end of Guam, has the colony with the greatest number of largest individuals. The maximum concentration of snails (about 10 per square foot) is found in the fairly level section of the stream, which is about 30 feet wide and half a foot deep. This area is only a few hundred feet from the high-tide mark of the ocean but is probably never diluted with salt water except perhaps during typhoons, which may come from the west.

Conditions at Agaña Spring, the most northerly located colony on the island, are interesting in the dwarfing effect on the size of the individuals. The spring is used as a source of water for nearby Agaña and at present has a pumping station located there. The spring proper is about 30 feet deep, with a diameter of about 60 feet. The upsurge of water is moderate, but the overflow is relatively fast, consisting of a 100-foot sluiceway about 3 or 4 feet wide. There are abundant algal growths in the spring. The shells and animals of this colony are similar to those of other Guam populations except in the reduction in size. No environmental cause for this could be found. Even more pronounced dwarfing is evident in specimens that were introduced to the large spring at Lithia, Fla.

On Leyte Island, Philippine Islands, where numerous collecting stations were made, *Thiara granifera* was found in large rivers and small streams. High in the central mountains, where large stream conditions duplicate those on Guam, colonies of this snail are rather common. In the extensive Leyte Valley, at the northeast end of the island, the larger rivers, with silty to sandy bottoms, meander; only rarely is *T. granifera* found along the very edges of the rivers, where the flow of water is moderately fast. However, smaller streams, which pass down from the foothills bordering the valley, are excellent habitats.

The water-temperature limits of this species were not appreciated until a survey was made of the Lithia Spring, Fla., populations. In aquaria and the spring, where the temperature remains around 76° F., the snails are able to maintain themselves in adequate numbers. However, just beyond the influence of the warm waters of the spring, where the cooler waters of the local river are about 50° F. or less, the snails are absent. The overflow ditch outside the extensive plant aquaria in Tampa is colonized by these snails during the warm summer months, but in winter, when the water temperature is as low as 50° F., these snails die off. The temperature recordings for Guam streams and even for the rivers at 3,000 feet altitude on Leyte Island were all above 75° F.

## BIONOMICS

Growth and size.—The rate of growth of the shell has not been determined, although, from common experience in raising these snails in aquaria, it is assumed that adult size or maturity is reached within 6 to 12 months. Two preliminary studies were made of the character of shell size, one on the 13 colonies collected on Guam Island, the other on the populations of Lithia Spring. In the latter study, dissections were made to determine the size at which individuals become sexually mature, for there is no tell-tale flaring or thickening to the outer lip that often accompanies maturity in many other molluscan species.

The significant differences in the size of samples taken at various places in the spring, only a few dozen yards from each other, are extremely important in demonstrating the wide range in size exhibited by one species. The aquarial stock from which these snails originated grew to a size almost four times that of its offspring in the spring. Only in an isolated, subsidiary spring, a few yards from the main spring, did specimens reach a size comparable to the aquarial stock. In all likelihood the differences in size exhibited by the seven sample populations in the spring have been brought about by ecological and not genetic factors. Not only are the means of shell lengths and maximum sizes of shell considerably varied, but the points at which maturity is reached are correspondingly shifted. This latter fact excludes the premise that these colonies represent aggregates of smaller, younger individuals. No direct correlation between diminutive size and type of bottom, depth of water, temperature of water, amount of shade, or distance from source of spring could be found. The small colony in the adjacent subsidiary spring attained a shell size nearly three times that of colonies in the main spring. Relatively few specimens per square foot were found in the smaller spring, while in the main spring overcrowding was evident, sometimes reaching a population density of 400 specimens per square foot. It is likely that food availability is the most important factor, but controlled experiments alone will support this assumption.

TABLE 3.—*Data pertaining to collections from Lithia Spring, Fla.*

| Station | Number of specimens | Mean shell length, mm. | Point of maturity | Type of bottom | Depth of water (ft.) | Distance from spring source (ft.) |
|---|---|---|---|---|---|---|
| 1 | 437 | 7. 88 | 7. 0 | Weed | 1 | 25 |
| 2 | 368 | 7. 50 | 5. 5 | Sand | 1–3 | 25 |
| 3 | 442 | 6. 28 | 5. 5 | Sand | 4 | 25 |
| 4 | 352 | 5. 55 | 6. 5 | Weed | 3 | 100 |
| 5 | 487 | 6. 30 | ? | Sand | 3 | 200 |
| [1] 6 | 23 | Insign. | ? | Sand | 10 | 500 |
| 7 | 676 | 9. 9 | 7. 0 | Sand | 2 | 30 |
| [1] 8 | 5 | Insign. | ? | Weed | 1 | 100 |
| [1] 9 | 4 | Insign. | ? | Weed | 2 | 250 |
| 10 | 105 | 5. 95 | 8. 0 | Weed | 1–4 | Subsidiary spring |
| [1] 11 | None | ------ | ---- | Weed | 1 | 250 |

[1] Insufficient numbers of specimens to ascertain maturity point or significant mean of shell length.

Table 3 shows the results obtained from 11 sample collections taken from Lithia Spring, Hillsborough County, Fla., in February 1947. The stations are marked on the map of the spring (fig. 41). Stations 6, 8, 9, and 11 had insufficient numbers of specimens to ascertain a reliable point at which maturity is reached, or a significant mean of shell length.

The map has been marked with short arrows, which indicate the main flow of the current of water coming from the spring and with long, broken arrows, which indicate the flow of river water that breaks across the low land to the north of the spring during flood periods. The river water, which is 18° C. in contrast to the 25° C. of the spring water, is fatal to these snails and undoubtedly accounts for their absence or low numbers at stations 8, 9, and 11. These last-mentioned stations are well stocked with local Florida snails (pleurocerids, amnicolids, and planorbids).

The mean shell-length data given in table 3 is of little value in making a comparison of two populations, and, in fact, can be very misleading. A look at the population-growth curves of shell length (fig. 42) will reveal the fallacy of the mean shell length. Most of the populations give a bimodal curve, as accentuated in population 4. The first peak is simply an aggregation of immature specimens, a factor that will vary according to the reproductive cycle of that population and that will change in value as the young grow to an adult size. In population 4, maturity is reached at 6.5 mm. and extends up to 12.5 mm. The mean for these adults, which are continually growing, is about 7.5 mm., yet if the entire population, both immature and adult specimens, is averaged, the mean must be recorded as 5.5 mm. This difficulty may be avoided in great measure by comparing only adults,

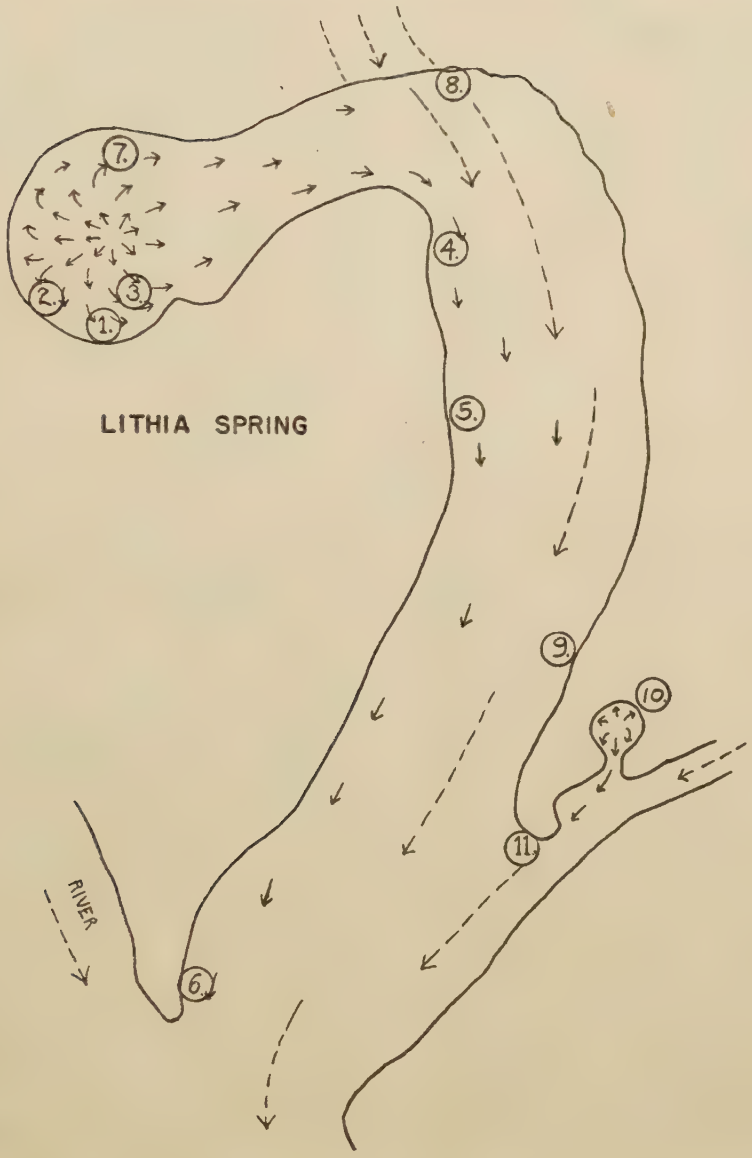


FIGURE 41.—Map of Lithia Spring, Fla., showing collecting stations (1 to 11) and water currents. Short arrows=spring water; long, broken arrows=river currents.

but, again, this is possible only if dissections can be made to determine whether the specimens in question are adult.

It is interesting to note the distance separating the mode of the immature curve and that of the adult curve in each population. Were these distances proportionately the same in each population, we could safely assume that the production of young was brought about simultaneously throughout the various populations of the spring and was

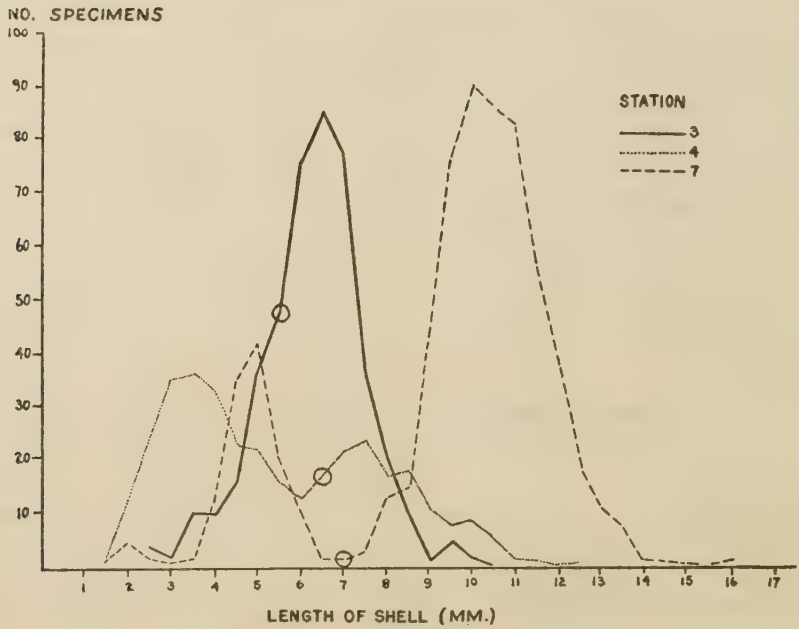


FIGURE 42.—Population curves based on shell length in three samples from Lithia Spring, Fla. Circles denote point at which maturity is reached.

due to a seasonal, environmental stimulus. However, the distance between the "wave" of young and the adults varies considerably from 6 mm. in population 7 to 0 mm. in population 3. The latter population, which is unimodal, may represent a population in which the "wave" of immature has grown into the mature class, and it is not unlikely that it was bimodal a few weeks before the date of collection, in the manner of the other populations.

The independent but pronounced production of young in the various populations suggests a cyclical activity in the physiology of the population itself, in which a fluctuation of sexual activity is present. How frequently these waves of young are produced could not be ascertained from data gathered on one visit to the spring.

McMullen (1947), in his studies on the growth rates of the freshwater snail *Oncomelania quadrasi* Moellendorff in the Philippine Islands, found similar smaller peaks or waves in the measurements of colonies. By revisiting his collecting areas periodically he was able to watch these waves of young move slowly toward the main peak of the adults. From his data he was able to ascertain that that species reaches maturity in 4 to 5 months. I have shown also (1946) that similar waves occur in the developmental stages of the eggs of *Oncomelania*, and that this was due to increased egg production brought about by the stimulus of rains and flood periods.

Bionomics of Guam colonies.—A natural sequence to the bionomic study of the Lithia Spring populations was an investigation of the same species living on Guam Island to see if similar environmental influences on size existed in areas natural to this species. In making a statistical study of the 13 colonies collected on Guam Island it was found that two serious drawbacks existed that, indeed, are common to any material of this nature. The first was that in most of the colonies an insufficient number of preserved animals were available to ascertain at what point maturity was reached. Secondly, the specimens were collected by hand and not in a strictly random fashion, as would be the case had a sieve or hand net been employed. The natural tendency of the collector is to choose the largest specimens first, then the smaller ones, until patience or time halts collecting.

Despite these handicaps, it was felt that a reliable index of size could be obtained by using the 10 percent of that part of the colony that represents the largest specimens. This method would be open to criticism were we dealing with animals which stopped growth at maturity, and which possessed some distinctive morphological adult character. When neither of these markers are present, as is the case with this genus of mollusks, we seek the maximum growth to which the snails grow and eliminate an abnormally low mean, owing to high percentage of young. The choice of the 10 percent figure is arbitrary, although, in population samples of 50 or more, the chances are that this will include only adults. It is unwise to choose simply the largest one or two specimens, for it is common knowledge that abnormal giants or perhaps polyploids are apt to be present in any population and will not serve as representatives. This is the reason why, in smaller samples, of 20 or less, it is best to choose the 20 or 30 percent representing the largest specimens, for comparative purposes.

What we are essentially seeking in a study of shell length is the largest size to which individuals will grow in any one population. Since growth is continuous throughout the life of the individual, two factors will delimit the length of shell—genetic and environmental. We have seen in our study of the Lithia Spring populations that some environmental factor is most likely responsible for length of shell, and it is not unreasonable to assume that such is the case in any differences found on Guam. On this island the streams are close to each other, and accidental dispersal by birds and other creatures is likely to keep the chances of a lengthy genetic isolation very low. To compare the 10 percent representing the largest specimens of each population is, in essence, to compare the ecologic conditions of each stream.

In order to test the validity of using the 10 percent referred to of each colony, histograms were made of the 13 colonies, and the means of shell length were calculated for the total population and for the top 10 percent. Figure 43 is a summation of this study from colonies A to

M, with the histograms in the right column and the means, to their left, represented by straight lines. The upper line is the mean for the entire population sample, and, the line below, the mean for the top 10 percent. These two lines could never have the same length, but the nearer they come together, the more natural will be the curve. Any preponderance of young would lower the mean for the entire population. It will be noticed, from a comparison of the proximity of the two means and the configuration of the histogram, that colonies such as A, B, E, and K, in which the two means are closest, have more compact histograms approaching the normal curve. (L is based on only 8 specimens and cannot be considered significant for this purpose.) On the other hand, samples D, F, and especially G and J, whose two means are relatively far apart, possess histograms that are considerably distorted and drawn out by a high percentage of young. A résumé of the statistics is given in table 4.

TABLE 4.—*Shell lengths of Guam colonies*

| Colony | Number of specimens | Mean of colony | Mean of largest 10 percent | Largest specimen |
|---|---|---|---|---|
| A | 92 | 13. 04 | 15. 3 | 16. 5 |
| B | 198 | 13. 44 | 16. 8 | 19. 0 |
| C | 100 | 15. 58 | 20. 1 | 23. 0 |
| D | 65 | 15. 10 | 22. 6 | 27. 0 |
| E | 50 | 19. 85 | 24. 0 | 26. 0 |
| F | 38 | 18. 44 | 25. 1 | 25. 5 |
| G | 97 | 15. 55 | 25. 4 | 27. 0 |
| H | 127 | 18. 33 | 27. 3 | 29. 0 |
| I | 20 | 22. 10 | 29. 2 | 30. 0 |
| J | 43 | 16. 09 | 31. 6 | 33. 5 |
| K | 245 | 24. 46 | 31. 7 | 34. 0 |
| L | 8 | 28. 68 | 34. 0 | 35. 5 |
| M | 36 | 26. 41 | 37. 1 | 40. 0 |

Although this method of comparing colonies lacks the usefulness and accuracy of presenting the true nature of each population, i. e., the percentage of young, the modes of one or more growth stages, and so forth, it seems to be the only recourse in problems confronting us in those invertebrates that show no morphological signs of maturity, and that grow throughout their life span. In reality, it answers only the question "how large does this species grow in this environment?"

A map of the southern half of Guam Island has been drawn and is presented in figure 40. The collecting localities for colonies A to M have been spotted, and the relative size of the top 10 percent of the individuals entered in the form of outlined shells. It will be noted that there is no geographical cline evident in their distribution. The only possible correlation noted is that between size of the large streams and size of large shells, but unfortunately insufficient studies of the

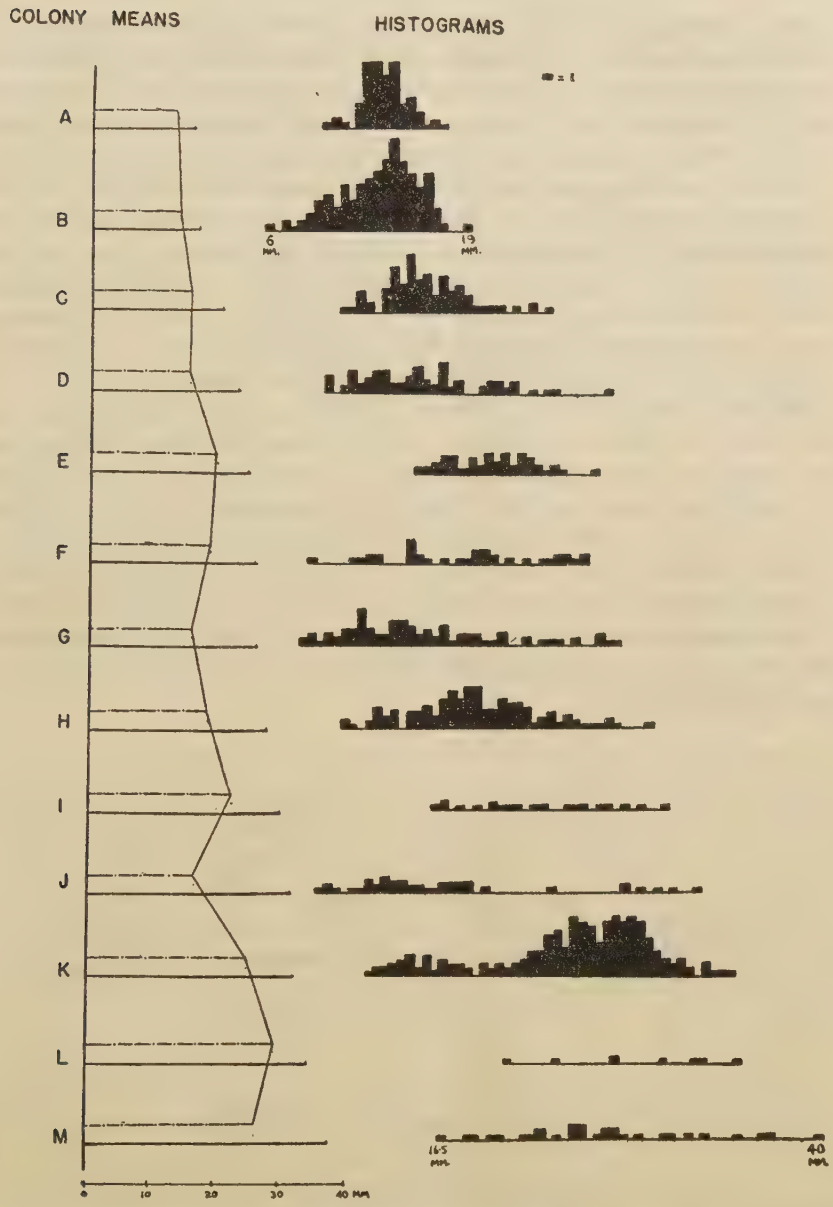


FIGURE 43.—Means and histograms of population samples from Guam Island (see p. 103 for explanation).

flow of these streams at various seasons were made. It would be interesting to mark and to transplant snails from, say, Agaña Spring to Umatac River to see if final growth conformed with the latter environment. A reciprocal transplant would be equally illuminating.

EFFECT OF EROSION ON SHELL LENGTH.—Whenever the water of the habitat of fresh-water mollusks becomes acid, there is apt to be a

marked effect on the shells and, in cases where the pH is less than 6.0, sometimes the death of the entire colony results. Many mollusks have developed a chitinous periostracum that protects the shell from corrosion. However, the abrasive action of sand particles and the attachment by algae or egg cases of *Neritina* gastropods may break through this outer covering and expose the calcium carbonate of the shell to the acid waters. It is not uncommon for some colonies of *Thiara granifera* to be considerably eroded at their spires. Shell-length measurements, in these cases, can hardly serve as fair comparisons with colonies that have suffered no loss of shell. The effect of erosion may be avoided by comparing the width of shells or the height of the last two or three whorls that have not been affected.

However, it is of equal interest to learn exactly what amount of reduction in length has been brought about by stream action, for ecologists may wish to know not only the pH values of various streams but also what effect acidity is having on the animals. A study was made of a population sample of 257 specimens of *Thiara granifera* (Naujan River, Mindoro Island, Philippine Islands, U.S.N.M. 258890) which showed considerable erosion. It was found that adults were reduced in shell length by 11.6 percent. Since this type of study has not, to our knowledge, been previously used, we have gone into considerable detail.

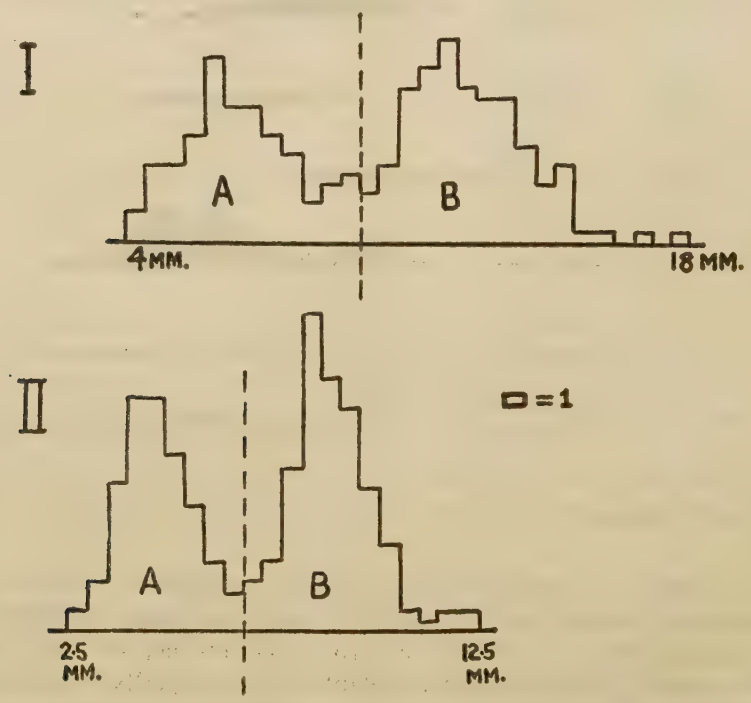


FIGURE 44.—I. Histogram of total shell length of sample from Mindoro colony. II. Histogram of same shells showing height of last whorl only.

Two histograms (fig. 44) are presented, with the upper one representing the distribution of individuals based on the measurements of total length of shell, and with the lower histogram representing the same individuals in which the height or length of the last whorl has been measured. Therefore, the upper histogram carries the effect of erosion, and the lower one is without it. Numerous small individuals were not worn away at their spires. These were measured for width and length to ascertain the ratio between these two figures (i. e., the obesity of the shell). The results are shown in table 5.

TABLE 5.—*Measurements of shells unaffected by erosion*

| Total length (mm.) | Length of last whorl (mm.) | Total length÷length of last whorl |
|---|---|---|
| 10. 5 | 6. 8 | 1. 55 |
| 9. 3 | 6. 0 | 1. 55 |
| 8. 5 | 5. 4 | 1. 56 |
| 8. 0 | 5. 4 | 1. 44 |
| 8. 0 | 5. 2 | 1. 53 |
| 7. 8 | 5. 2 | 1. 50 |
| 7. 0 | 4. 5 | 1. 55 |
| 6. 5 | 4. 6 | 1. 41 |
| 5. 8 | 3. 8 | 1. 52 |
| 5. 5 | 3. 6 | 1. 52 |
| | | Average ratio 1. 51 |

In a population sample, the distribution of which approaches the normal curve, or which consists of a uniform sample of adults, it would be necessary merely to multiply the mean of the last whorl measurements by 1.51 (total length/length of last whorl in perfect specimens) to arrive at a theoretical mean of the total shell length. Having obtained this figure, which would represent a population size unaffected by erosion, we need only to compare it with our actual measurements of eroded specimens to ascertain the amount of reduction.

This direct conversion could not be applied in this case, however, for the histogram is strikingly bimodal and in its lower peak possesses a number of young that were not worn away at the spires. The entire sample, therefore, was arbitrarily divided into groups A and B. As natural a midpoint as possible was chosen between the two peaks in the lower histogram at 6.75 mm. If the erosion-correction factor is applied to this (1.51 x 6.75), we obtain a theoretical equivalent total shell length of 10.19. It so happens that this figure divides the two groups in the upper histogram in exactly the same numerical proportion (i. e., 114 in group A and 142 group B) as we have in the lower histogram.

This division into two groups has put all the few perfect specimens in group A and has left us "adult" and all eroded specimens (except 1) in group B for comparative studies.

| | *Group A* | *Group B* |
|---|---|---|
| Total number | 114 (100%) | 142 (100%) |
| Not eroded | 31 (27.1%) | 1 (0.7%) |
| Eroded | 83 (72.9%) | 141 (99.3%) |

The means, their standard deviation, and the standard error of the means were calculated for the following:

TOTAL SHELL LENGTH

| | *Mean* | $\delta$ | $\delta_m$ | *N* |
|---|---|---|---|---|
| Group A | 6. 59 | 1. 42 | 0. 13 | 114 |
| Group B | 12. 46 | 1. 47 | . 12 | 142 |

LENGTH OF LAST WHORL

| | | | | |
|---|---|---|---|---|
| Group A | 4. 40 | 0. 29 | 0. 02 | 114 |
| Group B | 9. 03 | 1. 04 | . 09 | 142 |

The correction factor (length/width of perfect specimens) of 1.51 was then applied to the measurements of the last whorls in each group to compare theoretical total shell length and actual total shell length.

| | *Total length* | *Last whorl length* | *Last whorl × correction* | *Reduction caused by erosion* |
|---|---|---|---|---|
| A | 6. 59 | 4. 40 | 6. 64 | 0. 03 |
| B | 12. 46 | 9. 03 | 13. 63 | 1. 17 |

It will be noted that the reduction caused by erosion in group A is extremely small. This is due to the youth of the group, which has been exposed to erosion for a relatively short time. In fact, 27.1 percent of these specimens were without a trace of spire erosion. In group B, representing adults that have been exposed to acid waters for considerable time, the reduction has been 1.17 mm., or 11.6 percent.

## PARASITOLOGY

TREMATODE PARASITES.—This species of fresh-water snail is of particular interest to parasitologists because of its ability to serve as an intermediate host of numerous trematodes, three of which have been known, in their adult stages, to parasitize man. Other genera and species of the snail family Thiaridae also have this intermediate host ability, and their presence in the Orient is responsible for large endemic areas of the human lung fluke (*Paragonimus westermani*).

In the course of dissecting specimens from many localities, it was noted that some colonies in the Philippine Islands were infected as high as 20 percent with unidentified heterophyidlike cercariae. Dissection of specimens from the introduced colonies at Lithia Spring, Fla., failed to show any trematode infection.

A résumé of the parasites carried by this species is given here. Identification of the intermediate snail hosts as "*Melania obliquegranosa* Smith" is unquestionably referable to *Thiara granifera* (Lamarck). I have examined specimens with the above identification from Formosa Island and the illustrations published by Japanese parasitologists, and I find that the implicated Formosan species is a minor race of the widespread subspecies *T. g. mauiensis* Lea.

## Family HETEROPHYIDAE

### 1. HAPLORCHIS TAICHUI (Nishigori, 1924).

*Geographical distribution.*—Northern and central Formosa.

Implicated by Faust, E. C. and M. Nishigori, 1926.

*Intermediate snail hosts.*—*Thiara granifera* (Lamarck) (+*Melania obliquegranosus* (Smith)) and *Semisulcospira libertina* Gould.

*Second intermediate hosts.*—Fishes: *Cyprinus*, *Gambusia*, *Carassius*, *Zacco*, *Pseudorasbora*, *Phodeus*, *Ctenopharyngodon.*

*Definitive hosts.*—Birds (?), mammals, including man (experimental infection). An intestinal parasite acquired by eating raw, infected fish.

"The miracidium which hatches from the egg penetrates the tissues of the snail to which it is adapted, as in the case of the miracidial larva of *M. taihokui*, and metamorphoses into a sporocyst. Rediae are produced parthenogenetically within these sporocysts, and after a period of five to six weeks mature cercariae develop within the rediae. These carcariae erupt from the snail tissues and are found freely swimming about in the water." (Faust and Nishigori, 1926.)

### 2. DIORCHITREMA FORMOSANUM Katsuta, 1932.

*Geographical distribution.*—Formosa.

Implicated by Katsuta, 1932.

*Intermediate snail hosts.*—*Thiara granifera* (Lamarck), and *Semisulcospira libertina* Gould.

*Definitive hosts.*—*Mammals.* An intestinal fluke acquired by eating raw, infected fish.

### 3. METAGONIMUS YOKOGAWAI Katsurada, 1912.

*Geographical distribution.*—Japan, Korea, Formosa, Rumania, Siberia, Dutch East Indies, Palestine, Russia, and Spain.

*Intermediate snail hosts.*—*Thiara granifera* (Lamarck), *Semisulcospira libertina* Gould, *Hua amurensis* Gerstfeld. The record of "*Melania ebenina*" in China is probably referable to *Hua toucheana* Heude. Unknown in the Philippine Islands and Eurasia.

*Second intermediate hosts.*—Fishes: the salmonoid *Plecoglossus altivelis* and the cyprinoid *Richardsonium.*

## Family TROGLOTREMATIDAE

**4. PARAGONIMUS WESTERMANI Kerbert, 1878.**

*Geographical distribution.*—In the Orient, Japan, Korea, Manchuria, Formosa, China (especially Chekiang Province), French Indo-China, the Philippine Islands, Siam, the Malay Peninsula, Assam, India, New Guinea, Java, and Sumatra. Also South America, probably Africa, and one record for North America.

*Intermediate snail hosts.*—*Thiara granifera* (Lamarck) (Formosa), *Thiara* (*Melanoides*) *tuberculata* Müller (Formosa), *Semisulcospira libertina* Gould (Formosa and Japan), *Hua* species, and *Syncera lutea* A. Adams (China). Unknown elsewhere.

*Second intermediate hosts.*—The fresh-water crabs *Potamon* (*Geothelphusa*) *obtusipes* Stimpson, *P. dehaanii* White, and *Eriocheir japonicus* De Haan.

*Definitive hosts.*—Lungs of mammals, especially the felines and man.

The life cycle was first elucidated by K. Nakagawa in Formosa in 1917.

"When the snails are placed in water containing miracidia, the latter swarm around them and become attached to the heads, jaws and feet, but rarely to the tentacles and mantles. They cling with their suckers, insert proboscis into the tissue of the host and enter the body of the snail like the cercariae of Schistosomum [sic] japonicum, as described by Miyairi (1915). Unlike the miracidia of Schistosomum, those of the pulmonary distoma *Paragonimus* shed their cilia in this act.

"Besides the cercariae, sporocysts of various sizes are found abundantly in the liver of Melania [+*Thiara* and *Semisulcospira*]. They are sometimes found in the heart and kidneys." (Nakagawa, 1917, pp. 301–302).

Remarks on snail host specificity.—Gastropod mollusks serve as the obligatory first intermediate host of all digenetic trematodes or flukes. While in several cases the relationship between the parasitic fluke and the host snail is restricted to one species in certain areas, on the whole there does not appear to be any set pattern for certain snails to serve as hosts to any particular species or even genus of trematode.

Of the three important blood flukes that infect man, *Schistosoma japonicum* appears most restricted in its choice of only one genus of snails, *Oncomelania*. In the Philippine Islands, *Oncomelania quadrasi* Moellendorff is the only known carrier; in Japan, only *O. nosophora* Robson. This genus of snails is a gill-breathing amnicolid. Yet *Schistosoma mansoni* Sambon and *S. haematobium* Bilharz, of Africa and tropical America, are carried by the snails *Bulinus*, *Physopsis*, and *Australorbis*, all of which are lung-breathing Planor-

bidae. The phylogenetic relationships of these two groups of gastropods could hardly be farther apart. In all likelihood the choice of mollusks is based on the physiological adaptations and ecological preferences of the snails in each case.

*Thiara granifera* serves as host for two different superfamilies of trematodes, the Heterophyoidea (*Metagonimus*, *Haplorchis*, and *Diorchitrema*) and the Troglotrematoidea (*Paragonimus*). These same trematode groups are also carried by other genera of Thiaridae (*Semisulcospira*, *Hua*, *Goniobasis*, and the subgenus of *Thiara* called *Melanoides*). In addition, however, members of the snail families Amnicolidae and Synceridae may also act as intermediate hosts, in some cases being the only snail hosts in the local endemic area.

In all likelihood *Thiara granifera* may be considered a potential host of the American *Paragonimus kellicottii* on epidemiological and ecological grounds.

An understanding of snail-host specificity will probably not arrive from a study of molluscan phylogeny, but rather will have to await an intensive study of the physiology of the many fresh-water species that serve as hosts. The seeming tendency for certain families of snails to serve as hosts to particular groups or species of flukes is probably merely an expression of a common physiological condition possessed by these snails.

## INTRODUCTION INTO THE UNITED STATES

*Thiara granifera* has established itself some 5,000 miles east of its normal geographical limits in the Lithia Springs of Hillsborough County, Fla. The thriving American colonies should be considered as potential hosts for one or more of the trematodes that they are capable of carrying in their native habitats. (See under Parasitology, p. 109.) It appears, however, for the several reasons discussed subsequently, that no danger exists in the establishment of these snails in our country.

It appears from the information now at hand that there was only one introduction of the snail into the United States. On March 23, 1935, an aquarium dealer of San Francisco, Calif., sent four specimens to the United States National Museum for identification. In a letter (March 23, 1935) to Dr. G. S. Myers, then curator of the division of fishes, this dealer states, "I do not know just where their native habitat might be, because here and there, from different points, Australia, China, Hawaii, etc., where I get a small shipment, plant life comes along and some small ones [snails] may be adhering to it."

No further notice was taken of this species, since at that time the parasitological importance of this species was overlooked. It was not until 1947 that it reappeared, when Dr. C. Wythe Cooke, of the U. S. Geological Survey, collected a number of specimens in Lithia Spring,

Fla., and kindly forwarded them to the United States National Museum. A few weeks later I was sent to this spring to determine its prevalence, manner of introduction, and its possible spread.

*Thiara granifera* is present in the main Lithia Spring in extraordinary numbers, sometimes as many as 400 specimens per square foot. A small, connecting subsidiary spring contains a few larger individuals. A fuller account of the spring condition appears in the section on bionomics (p. 100).

An aquatic-plant and fish dealer in Tampa related that he acquired specimens in 1937 while on a visit to California. Since that time, his plant vats have been stocked with this mollusk which, as an oddity, had been sold over a hundred times in a year as the "Philippine horn of plenty." It was his opinion that the snails were probably accidentally introduced to the spring around 1940, when improperly washed tubs were used to gather native plants. I have seen specimens in home aquaria in Silver Spring, Md., which had been acquired from Washington, D. C., dealers.

It will be seen by the above experiences that any foreign snail that has sales value because of its attractive appearance or peculiar habits will soon be distributed to many parts of the country and in many cases will be introduced purposely or accidentally to native waters. Probably the most likely solution to the problem of controlling introduced, dangerous mollusks lies in encouraging dealers, particularly the importers, to send their mollusks for identification to museums that have specialists in mollusks on the staff. The present programs of the Bureau of Plant Quarantine and Insect Control and the United States Public Health Service appear to be extensive enough for our protection. It must be realized that even the most stringent of laws prohibiting the import of foreign mollusks are not going to offer perfect screening, since accidental introductions by various means are likely to occur. In the past hundred years approximately 50 species of exotic species of land and fresh-water mollusks have established themselves in the United States and Canada.

The geographical origin of these snails will probably remain uncertain. From the condition and size of individuals in the Lithia Spring colonies, it appears that an abnormally stunted ecological form exists, which makes fair comparisons with races from endemic Pacific areas difficult. The more closely resembling lots in the United States National Museum are from the Hawaiian and Marianas Islands. They are possibly members of the subspecies or geographical race *Thiara granifera mauiensis* Lea, 1856.

It is highly unlikely that this snail will spread to many other sections of the United States, except in rare spring localities where water

temperatures remain above 75° F. Its public health menace is negligible by virtue of the complex life cycle of the parasite that it is capable of carrying. A second intermediate host, usually a freshwater crayfish or crab, is a necessary part of the life cycle of *Paragonimus*. Furthermore, in order to accomplish infection of the definitive host the crayfish must be eaten raw, a custom which is infrequent or rare among our people.

## IDENTIFICATION OF THIARA GRANIFERA AND CLOSELY RESEMBLING SPECIES IN THE UNITED STATES

In addition to a snail of similar appearance, which is native to Florida springs, there are two species of thiarid snails sometimes found in aquaria that are likely to be confused with *Thiara granifera*. *Pleurocera* (or *Ceriphasia?*) *catenaria* (Say) is found in the same habitat as *T. granifera* at Lithia Spring, but rarely succeeds in an aquarium. *Hemisinus cubanianus* (Orbigny), from Cuba, and *Pachychilus glaphyrus* (Morelet), from Central America (Honduras), have been raised by fish fanciers with moderate success. The synopses of distinguishing characters presented herewith will aid in identifying these species.

### THIARA (TAREBIA) GRANIFERA (Lamarck)

FIGURE 45, *a*; PLATE 8, FIGURES 1, 2

At Lithia Spring: Shell 10 to 15 mm. (about ½ inch) in length, amber to reddish amber, rarely with green algal attachments. Sides of whorls in spire flat, without strong spiral cords.

In aquaria: Shell sometimes 20 mm. in length, and if in stagnant tank, heavily varnished with black coating. Animal with young in brood pouch under skin of back; mantle edge with tiny, fleshy fingers or papillae. Operculum with nucleus at one end.

### PLEUROCERA CATENARIA (Say)

FIGURE 45, *c*; PLATE 8, FIGURES 3, 4

Shell 15 to 20 mm. (about ¾ inch) in length, amber brown to black-brown, often with green algal attachments. Sides of whorls in spire slightly rounded and carinate near the bottom, with strong spiral cords, which form well-developed tubercles as they cross the small axial ribs. Often with dark brown, spiral color band at base of shell. Mantle of animal wavy, but without papillae. No brood pouch. Operculum with nucleus near center.

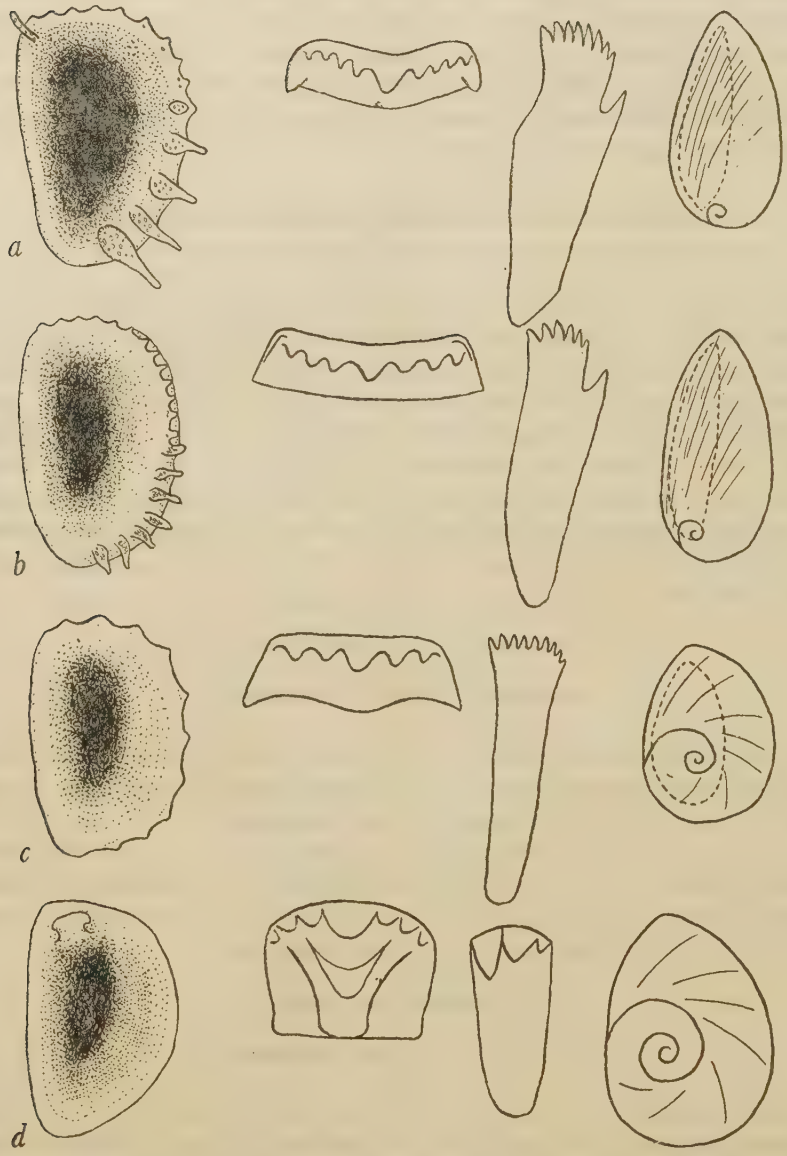


FIGURE 45.—Animal characters of four genera of Thiaridae: *a*, *Thiara* (*Tarebia*) *granifera* (Lamarck), from Lithia Spring, Fla., and the Orient; *b*, *Hemisinus cubanianus* (Orbigny), from Cuba; *c*, *Pleurocera catenaria* (Say), from Florida springs; *d*, *Pachychilus glaphyrus* (Morelet), from Honduras. (From left to right: Mantle edge, central radular tooth, outer marginal tooth, and operculum.)

### HEMISINUS CUBANIANUS (Orbigny)

FIGURE 45, *b*

Shell 20 to 25 mm. (about 1 inch) in length, smooth, greenish brown, with many spiral rows of elongated, black-brown color spots. Animal with a few, large young in brood pouch under skin or back. Mantle edge with tiny, fleshy papillae. Operculum with nucleus at one end.

### PACHYCHILUS GLAPHYRUS (Morelet)

FIGURE 45, *d*

Shell 35 to 45 mm. (about 1½ to 1¾ inches) in length, smooth, black-brown, and without spiral rows of color dots. Animal without brood pouch. Mantle edge smooth. Operculum with nucleus near center.

## LITERATURE CITED

ABBOTT, R. T.

1946. The egg and breeding habits of *Oncomelania quadrasi* Mlldff., the schistosomiasis snail of the Philippines. Occ. Papers on Mollusks, Harvard Univ., vol. 1, No. 6, pp. 41–48, pl. 9.

1948. Handbook of medically important mollusks of the Orient and Western Pacific. Bull. Mus. Comp. Zool., vol. 100, pp. 245–328, 5 pls., 14 figs.

1948a. A potential snail host of Oriental schistosomiasis in North America (*Pomatiopsis lapidaria*). Proc. U. S. Nat. Mus., vol. 98, pp. 57–68, pls. 3–4.

ABBOTT, R. T., and HUNTER, G. W., III.

1949. Studies on potential snail hosts of *Schistosoma japonicum*. I. Notes on the amnicolid snails *Blanfordia*, *Tricula* and a new genus, *Fukuia* from Japan. Proc. Helminth. Soc. Washington, vol. 16, No. 2, pp. 73–86, 3 pls.

BOUVIER, M. E. I.

1887. Systéme nerveux morphologie generale et classification des gasteropods prosobranches. Ann. Sci. Nat. Zool., vol. 3, No. 7, pp. 1–510, pl. 1–19.

FAUST, E. C. and M. NISHIGORI.

1926. The life cycles of two new species of Heterophyidae, parasitic in mammals and birds. Journ. Parasit., vol. 13, no. 2, pp. 91–128.

MCMULLEN, D. B.

1947. The control of Schistosomiasis Japonica. I. Observations on the habits, ecology and life cycle of *Oncomelania quadrasi*, the molluscan intermediate host of *Schistosoma japonicum* in the Philippine Islands. Amer. Journ. Hygiene, vol. 45, pp. 259–273.

MOORE, J. E. S.
1889. *Nassopsis* and *Bythoceros*. Quart. Journ. Micr. Sci., new ser., vol. 17, pp. 187–201, pl. 20–21.
1899. *Tanganyika rufifilosa*, and the genus *Spekia*. Quart. Journ. Micr. Sci., new ser., vol. 42, pp. 155–185, pls. 20–21.
1898. The anatomy of *Typhobias*, with a description of the new genus *Bathanalia*. Quart. Journ. Micr. Sci., new ser., vol. 41, pp. 181–204, pl. 11–14.

NAKAGAWA, K.
1917. Human pulmonary distomiasis caused by *Paragonimus westermanni*. Journ. Exper. Med., vol. 26, pp. 297–323.

RIECH, E.
1937. Systematische, Anatomische, Okologische und Tiergeographische Undersuchungen über die Süsswassermollusken Papuasiens und Melanesiens. Archiv für Naturg., new ser., vol. 6, No. 3, pp. 35–153.

SESHAIYA, R. V.
1929. The stomach of *Paludomus tanschaurica* (Gmelin). Rec. Indian Mus., vol. 31, pp. 7–12.
1934. Anatomy of *Paludomus tanschaurica* (Gmelin). Rec. Indian Mus., vol. 32, pt. 2, pp. 185–212, 15 figs.
1940. A free larval stage in the life-history of a fluviatile gasteropod. Current Science, vol. 9, No. 7, pp. 331–332. Calcutta.

THIELE, J.
1929. Handbuch der systematischen Weichtierkunde, vol. 1, 376 pp. Jena.

WENZ, W.
1939. Handbuch der Paläozoologie, vol. 6, Gastropoda, part 3: Prosobranchia, pp. 481–720. Berlin.

U. S. GOVERNMENT PRINTING OFFICE: 1952

1, 2. Shells of *Thiara* (*Terebia*) *granifera* (Lamarck), from Lithia Springs, Fla. (× 5).
3, 4. Shells of *Pleurocera catenaria* (Say), from Lithia Spring, Fla. (× 4).

THIARA (TEREBIA) GRANIFERA (LAMARCK).
Contents of a brood pouch, showing development from egg to young ready to emerge. (× 25).